

On their way to the north: larval performance of Hemigrapsus sanguineus invasive on the European coast—a comparison with the native European population of Carcinus maenas

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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 15-24°C) and two food conditions (permanent vs daily limited access to food). Larval survival of H. sanguineus was low at 15 °C and increased with temperature, in contrast to the high survival reported for C. maenas larvae in the range 15-24 °C. 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 (24°C) 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

58 INTRODUCTION

59 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; 60 61 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, 62 63 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 64 65 community, and an increase in the homogeneity of the invaded communities (Rahel 2000; Pyšek et al. 66 2012; Geburzi et al. 2018). Whenever the "introduced" species causes an impact on the host ecosystem, 67 it is considered "invasive". Biological invasions are one of the most important threats to biodiversity 68 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 69 70 (Hulme 2017), by means of different interactions including competition, predation, and introduction of 71 new diseases (Ruiz et al. 2000; Sakai et al. 2001; Jeschke et al. 2012). Biological invasions have been 72 reported for most marine and estuarine habitats in the world (Katsanevakis et al. 2013; Chan and Briski 73 2017; Pyšek et al. 2020). Many hypotheses have been proposed to explain biological invasions and the 74 success of the invaders (Simberloff and Von Holle 1999; Gurevitch et al. 2011; Kelley 2014), yet there 75 is still little information on the processes involved in dispersion and establishment of alien species in 76 novel habitats (Bailey et al. 2020; Rato et al. 2021).

77 Global climate change is causing an increase in the number and the impact of biological 78 invasions (Hulme 2017; González-Ortegón et al. 2020; Pyšek et al. 2020), because of the steady increase 79 in temperature (IPCC 2021), and the increased frequency of extreme events (e.g. heatwaves, Meehl and 80 Tebaldi 2004; Smale et al. 2019). These changes combined with other human activities can act together 81 to help the dispersal and establishment of new species. For example, the ovster *Crassostrea gigas* was 82 first introduced in the North Sea for aquaculture purposes and was able to establish there due to above-83 average summer temperatures that helped the species to spread (Diederich et al. 2004; Smaal et al. 84 2009). Global warming has also led to the poleward expansion of many species (Sorte et al. 2010; 85 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

93 may particularly impact life history stages characterised by high growth rates (Foster and Hirst 2012; 94 Otto et al. 2020). Crustacean larvae are an example where high growth rates are sustained by high 95 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 96 97 growth rate and survival (Torres and Giménez 2020). However, the nature of the effect could vary 98 between native and exotic competitors because of differences in thermal optimum ranges (Griffith et 99 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 100 species. 101

The Asian shore crab *Hemigrapsus sanguineus* is native to the east coast of Asia (20° - 50° N) 102 103 (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). 104 It has successfully invaded the coasts of North America, North Europe, and the Adriatic and Black Seas 105 106 (Schubart 2003; Micu et al. 2010) via ballast water (Ai-yun and Yang 1991; Kraemer et al. 2007; 107 Epifanio 2013). In northern Europe, H. sanguineus was first recorded in France and the Dutch Delta 108 system in 1999 (Breton et al. 2002) and then spread to the North Sea and Scandinavia (Wolff 2005; 109 Kerckhof et al. 2007; Dauvin and Dufossé 2011; Gittenberg et al. 2010; Gothland et al. 2013; Seeley et 110 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; 111 GBIF.org). There are several factors likely to drive or limit the expansion of *H. sanguineus*, including 112 113 the presence of congeneric competitors (e.g. US North Pacific, Steinberg and Epifanio 2011, Lord 2017) 114 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 115 temperatures (Epifanio et al. 1998; Stephenson et al. 2009). Hence, as a result of warming, the 116 117 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 118 119 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 120 juveniles affecting their recruitment success (Lohrer and Whitlach 2002; Jensen et al. 2002; Geburzi et 121 122 al. 2018). For example, in Southern New England H. sanguineus has significantly reduced the 123 recruitment of C. maenas due to direct predation, leading to a decline in densities by 40 - 90 % (Lohrer 124 and Whitlatch 2002). In addition, when in sympatry individuals of C. maenas migrate towards the 125 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. 126

We compared the performance of *H. sanguineus* and *C. maenas* from the perspective of thelarval phase for co-occurring populations of the German Bight (Helgoland, North Sea). We focus on

129 larvae because larval survival and recruitment are critical contributors to the propagule pressure by H. 130 sanguineus (Simberloff 2009) and for the persistence of populations of C. maenas. Propagule pressure, 131 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, 132 133 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 134 and Sponaugle 2009; Pineda et al. 2009; Giménez et al. 2020). In particular, differences in larval 135 survival among co-occurring species may affect the balance of competition, either exacerbating or 136 counteracting the outcome. In theory, counteracting effects may occur in cases of trade-offs between 137 competition and dispersal abilities (Seifan et al. 2013). Because *H. sanguineus* was first reported in the 138 German Bight very recently (2008- Scrosati et al. 2011, 2009- Jungblut et al. 2017), it is not clear yet 139 140 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 °C (Epifanio 2013) which 141 characterise the spring and early summers in the German Bight and coastal North Sea (Giménez et al. 142 143 2020). For H. sanguineus, larvae appear to be released when the temperature surpasses 15 °C which is early/mid-June depending on the year (Giménez et al. 2020). In the case of C. maenas, larval release 144 145 starts in May (Harms et al. 1994), but the full larval season of both species partially overlap. We know 146 that under food limitation, zoea I of *H. sanguineus* is more tolerant to short thermal fluctuations than 147 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 148 in C. maenas. 149

150 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 151 quantified the combined effects of temperature and food limitation on survival and performance of 152 153 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 154 155 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-156 157 metamorphic stages in the benthic habitat (Giménez et al. 2004; Pechenik 2006; Giménez 2010; Torres 158 et al. 2016). Second, we compared our results on *H. sanguineus* with those obtained by Torres and 159 Giménez (2020) for a co-occurring population of C. maenas.

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163 MATERIALS AND METHODS

164 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 μ m) seawater (32.5 ‰) permanently aerated, in a temperature-controlled room at 18 °C (± 0.5 °C) 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.

171 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 172 173 Giménez 2020). This experimental procedure was repeated four times, i.e. once for each of the hatches 174 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 175 treatment, see below for more details), combination of 2 levels of daily access to food (6 or 24 h / day, 176 177 provided *ad libitum*) and 4 temperatures (15, 18, 21 and 24 °C). The different temperatures were chosen based on its natural variability in the German Bight: 15 and 18 °C represent temperatures recorded 178 during the larval season of H. sanguineus (Giménez et al. 2020); this corresponds to summer 179 180 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 181 182 consequence of the expected increment in the frequency of warm summers (Christidis et al. 2015).

183 Experiments were carried out in temperature-controlled rooms and using natural UV-treated 184 filtered (0.2 µm) seawater. When hatching occurred, 50 larvae were sorted into each of 500-mL rearing 185 vessels (4 replicate vessels per treatment for each of the four females) in UV-treated filtered seawater 186 at the temperature of hatching. Freshly hatched Artemia sp. nauplii (Great Salt Lake Artemia, Sanders, 187 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 9 188 189 a.m. and 3 p.m., following Giménez and Anger 2005, Torres and Giménez 2020). By contrast, in the 190 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 191 192 daily water change, live larvae were staged and recorded, dead ones were also recorded and removed 193 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

- 204 analyser, Elementar Analysensysteme).
- 205

206 Data analysis

207 The response variables were survival, duration of development, body mass, elemental 208 composition (carbon and nitrogen), and instantaneous growth at the megalopa. Survival to each zoeal 209 stage was calculated as the percentage of survivors in relation to the number of organisms at the start 210 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 211 212 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 213 214 development of each individual megalopa.

Mixed modelling was carried out in R (function lme and gls from package nlme, Pinheiro et al. 215 2018, R Core Team 2013) to assess the responses to the different combinations of food availability and 216 temperatures on survival and duration of development. The models contained temperature and food 217 availability as fixed factors and female of origin as a random factor. We performed backwards model 218 selection (Zuur et al. 2009) in two steps. In a first step, we tested the random terms using restricted 219 220 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 221 222 analysis. When the difference between two models was $\Delta AICc < 3$ and the most complex model had 223 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 224 significant we chose the simpler model (with the lowest number of parameters). In a second step, the 225 226 fixed terms were analysed through maximum likelihood (ML). For dry mass, elemental composition, 227 and growth rates at the megalopa we did not get sufficient data in the food limited treatment at 15 °C 228 for female 4 (F4). We therefore, analysed the data using two different starting models: (1) considering 229 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.

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241 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.

249 We also calculated the ratios of survival (S_R) and growth rates (G_R) between species, i.e. as SR $=S_{\rm H}/S_{\rm C}$ and $G_{\rm R}=G_{\rm H}/G_{\rm C}$, where $S_{\rm H}$ and $S_{\rm C}$ are the survival to the megalopa of *H. sanguineus* and *C.* 250 maenas, respectively and G_H and G_C the respective growth rates (from hatching to megalopa). We 251 252 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 253 254 variation in survival and growth associated to variations within and among families. First, for each 255 species, we simulated 1000 values of the survival and growth rates. Survival was simulated from the 256 statistical model fitted to the responses of both species to the different combinations of temperature and 257 access to food; i.e. there were 1000 values for each combination of species, response variable, 258 temperature, and food condition. Growth was simulated from an additional statistical model which also 259 considers survival as covariate; this model incorporates correlations between average survival and 260 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 261 was that of Tables S2; for growth we fitted an additional model based on female-to-female averages 262 263 (Supplementary material, Materials and Methods, Section 2. Data analysis: details on model 264 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 265 and food condition a pair of values of survival and growth was randomly sampled (function sample, R 266 Core Team 2013) for each female of each species. The ratio of survival (or growth) was calculated 267 between two randomly chosen females (one per species). This procedure was repeated 4000 times in 268

- 269 order to obtain distributions of ratios of survival (and growth) for each combination of temperature and
- 270 food condition. We then calculated the average of four ratios, comparing the performance of four
- 271 hatches of *H. sanguineus* and four of *C. maenas*; this calculation takes into account that larvae obtained
- 272 from four different females were used for each study. In addition, this procedure to calculate the average
- 273 maintained the correlation between survival and growth. Using the simulated ratios of survival and
- 274 growth, we calculated the centroid and the 90% confidence ellipses which were plotted for each
- combination of temperature and food (see Fig. 5).

277 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.

283 Survival, development, and growth

Survival to megalopa in *H. sanguineus* decreased towards lower temperatures and under limited 284 access to food (Fig. 1, left panel); while at 15 °C, food limitation reduced survival by 74 %, at 24 °C 285 the survival reduction was 35 %. Best models retained food availability and temperature operating in 286 287 additive or interactive ways depending on the stage (Table S3), but with variations among larvae from 288 different females (Table S4). Survival to megalopa under limited access to food ranged from 0 - 74 % 289 depending on temperature and female of origin, with 0 % survival occurring at 15 °C and 24 °C for 290 female 3 (Fig. S5). The effects of temperature and limited access to food on survival to zoeae II to IV 291 were small, but increased for survival to ZV and especially to the megalopa (Fig. S6). The sensitivity 292 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 293 294 the female (Fig. S5).

295 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 296 logarithmic scale: Table S3). The multiplicative model can be illustrated considering the combination 297 of 24 °C and permanent access to food as the optimal condition. In this case, the observed proportion 298 of survivors under the combination of two stressors experienced simultaneously (15 °C and limited 299 300 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 °C: 0.2). On a female-by-female 301 basis, the effects ranged from synergistic with a strong effect of temperature (F1 and F2) to antagonistic 302 303 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).

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Duration of development to megalopa in *H. sanguineus* increased with decreasing temperatures 319 320 in a non-linear pattern (Fig. 2a, left panel); the best model retained the interactive effect of temperature 321 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 322 323 between the two food conditions). However, at 21 and 24 °C the delay was longer than 3 days, representing 14 - 16 % change (Fig. 2a, left panel). The effect of food limitation was weak at early 324 stages and then it became stronger in the zoea IV (Fig. S7); best models retained temperature in 325 development to stages ZII and ZIII, temperature and food availability operating in an additive way in 326 327 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. 328

329 Carbon growth rates of H. sanguineus increased with increasing temperatures in both food 330 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 331 332 temperature (Table S6). Similar effects were also found in terms of dry mass and nitrogen content (Fig. 333 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 334 335 females. Best models retained food availability and temperature operating interactively (Table S6). 336 Consistently for all females, the effect of food limitation on carbon content was strong in the range 15

- 21 °C as compared with 24 °C (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 °C 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 342 temperature which contrasts to those of C. maenas, that are more sensitive to food limitation (Fig. 2). 343 In terms of duration of development, larvae of *H. sanguineus* were more sensitive to temperature than 344 C. maenas, especially at low temperatures; at 15 °C H. sanguineus reaches the megalopa in ca 70 days 345 while C. maenas needs ca 30 days (Fig. 2a). By contrast, limited access to food increased developmental 346 time in a lesser extent in *H. sanguineus* (< 16 % change between the two food conditions) than in *C.* 347 maenas (> 20 %). While growth rates of *H. sanguineus* increased with temperature irrespective of the 348 food condition, those of C. maenas decreased with temperature but remained constantly low in the food 349 limited treatment (Fig. 2b). H. sanguineus megalopa had higher carbon content and lower C/N ratios 350 than C. maenas (Fig. 2d). The weakest effect of food limitation on carbon content found at the highest 351 352 temperature in *H. sanguineus* contrasts to the pattern found in *C. maenas*, where the effect was weakest

at the lowest temperature (Fig. 2c).

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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.

362 Integrated growth responses to megalopa of *H. sanguineus* were characterised by a strong 363 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 364 permanent access to food larvae reached a maximum threshold of body mass (= 260 µg/ ind), and 365 366 differences between food conditions were small (limited access to food = $240 \,\mu\text{g/ind}$). However, lower thresholds were reached at lower temperatures, especially under limited food availability (Fig. 3, upper 367 side of graph). In addition, H. sanguineus larvae did not compensate for the effect of low temperature 368 on body mass even under permanent access to food (Fig. 3, upper side of graph). Similar patterns 369 characterised the integrated responses in terms of carbon and nitrogen content (Fig. S9). 370



Figure 3. *Hemigrapsus sanguineus* and *Carcinus maenas*. Integrated responses of body mass and duration of development

- 373 under the different treatments of temperature and food availability. Data shown as average values \pm SE for both variables.
- 374 Symbols: permanent access to food is represented with blue symbols (indicated as `+') and limited access to food with green
 375 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:

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

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.



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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.

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430 DISCUSSION

There were three main findings out of our experiments. First, Hemigrapsus sanguineus is able 431 432 to metamorphose to megalopa under limited daily access to food over a wide thermal range (15 - 24 °C). Second, within the range of temperatures experienced in the local habitat (German Bight, North 433 434 Sea), low temperature (15 °C) appears to be the primary limiting driver of larval performance, in terms 435 of survival and growth. Third, when the performance is quantified in relation to that of Carcinus 436 maenas, unfavourable scenarios for H. sanguineus are projected for temperature characterising cool 437 summers. In turn, favourable scenarios are projected for summers characterised by long heatwaves and 438 after coastal warming.

439 Temperature and food limitation

H. sanguineus larvae were able to metamorphose to megalopa under limited access to food over 440 441 a wide range of temperatures, with some variations among families (i.e. larvae originated from different 442 females). This is consistent with other studies on decapod crustacean larvae and strengthen the general 443 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 444 2014; D'Urban Jackson et al. 2014; Torres and Giménez 2020). Limited daily access to food is expected 445 446 in habitats characterised by food patchiness (Paffenhöfer et al. 1987; Durham and Stocker 2012; Prairie 447 et al. 2012, Robinson et al. 2021) and in scenarios where larvae perform diel or tidal migrations 448 (Forward et al. 2001; Queiroga and Blanton 2005; dos Santos et al. 2008, Thygesen and Patterson 2019). 449 In temperate latitudes such as the one of the German Bight, access to prey during nigh time should be 450 limited to a few hours because H. sanguineus larvae develop in summer when the darker period is 451 restricted to few hours. Hence, H. sanguineus, as other species including C. maenas should be able to 452 survive the larval phase as long as they access prey for a limited amount of time every day.

453 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 454 complex life cycles, traits at metamorphosis are relevant for post-metamorphic survival and are the 455 basis for trait-mediated effects of the pelagic environment on recruitment in the benthic habitat 456 457 (Giménez 2004; Pechenik 2006; Marshall et al. 2008; Torres et al. 2016). Larvae of H. sanguineus 458 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 459 expected for cool and warm summers. It is important to understand the mechanisms driving body size 460 461 at metamorphosis as they should mediate effects of warming on species responses (Lowe et al. 2021; 462 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 463 464 handful of studies have investigated how such mechanisms respond to warming (D'Urban et al. 2014;

465 Torres and Giménez 2020; Griffith et al. 2021). Body mass is a plastic trait, driven by variations in 466 larval growth rates and developmental time, but body mass should vary within upper and lower 467 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 468 to achieve a large body mass (e.g. predation). Longer developmental time contributes to larger body 469 mass but also determines the period when larvae are exposed to pelagic mortality risks (Eckert 2003) 470 471 and the conditions experienced after settlement (Miron et al. 1999; Jarrett 2003). Because postsettlement conditions fluctuate in seasonal environments, the specific conditions experienced by 472 juveniles are indirectly determined by the duration of the larval phase. For instance, in *H. sanguineus*, 473 474 late settlement may result in reduced juvenile growth as individuals may miss most of the summer 475 season where growth rates are enhanced by high temperatures in the intertidal zone. During summers, 476 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 477 2002). In addition, late settlement may expose individuals to cannibalism (Moksnes et al. 1997; 478 479 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 480 481 variation; because of trade-offs associated to such costs, the less responsive traits should be those with 482 higher associated costs (Gotthard and Nylin 1995; Gotthard 2000, 2004). In the case of H. sanguineus, 483 larvae responded to food limitation mainly through reduction of growth rates; the extension of 484 development time, found to partially compensate effects of food limitation in C. maenas (Torres and 485 Giménez 2020) was rather short. By contrast, H. sanguineus larvae showed a strong plasticity to 486 temperature by extending the development from < 20 days at 24 °C to > 60 days at 15 °C. Given that at the local population, H. sanguineus females appear to release larvae in early summer, only after 487 temperatures reach 15 °C (Giménez et al. 2020), summers with water temperatures in the range of 15 -488 489 18 °C would result in late settlement if larvae were to extend further the developmental time. Hence, in the range 15 - 18 °C and under food limitation, further extension of the larval phase may have higher 490 491 fitness costs than metamorphosing with a smaller size (but profiting from a warm growing period).

492 Low temperatures

493 Our study is in line with others (Stepherson et al. 2009; Giménez et al. 2020), showing that low 494 larval survival occurs at low temperatures (range 12 - 15 °C). Reduced body mass at metamorphosis 495 found at 15 °C is expected because body mass at stage, peaks at temperatures where physiological 496 performance is optimal (Anger 1998; Anger 2001). Perhaps the body mass of megalopa of *H.* 497 *sanguineus* would decrease at temperatures higher than 24 °C, as expected from the temperature-size 498 rule (Atkinson 1994). 499 Under low temperature and food limitation, larvae hatching from all females showed a stronger 500 reduction in nitrogen as compared to carbon. This is unlike previously observed responses to stressors 501 in other species (Harms et al. 1994; Torres and Giménez 2020; Torres et al. 2021) where the main 502 characteristic is a stronger reduction in carbon than in nitrogen content. In decapod crustaceans, carbon 503 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 504 to sustain activity or the enzymatic machinery. Given that in decapods, nitrogen is a proxy for protein 505 levels, we hypothesise that the reduction observed in *H. sanguineus* reflects a thermal limitation in the 506 507 rate of protein synthesis. Protein synthesis accounts for a great proportion of the specific dynamic action 508 (SDA, Brody 1964) in crustaceans, i.e. the energetic costs incurred by physiological processes related 509 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 510 maenas, protein synthesis accounts for 20-37 % of the post-meal oxygen rise (Houlihan et al. 1991). 511 Temperature affects rates of protein synthesis in fasted and inactive crustaceans (McMillan and 512 Houlihan 1988; Whiteley et al. 1996; El Haj and Whiteley 1997). Hence, one would expect that rates 513 of protein synthesis are compromised at lower than optimal temperatures, due to limitations in covering 514 the associated costs (Whiteley et al. 1997, 2001). In this study, the lowest temperatures tested are 515 516 suboptimal for *H. sanguineus*, but not for species that are native to North European Seas (e.g. D'Urban 517 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 518 519 thermal tolerance range.

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

522 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 523 outcome of the balance between larval settlement, and competition between C. maenas and H. 524 sanguineus in the benthos. C. maenas larvae can complete larval development at temperatures as low 525 526 as 12 °C (Dawirs 1985; Nagaraj 1993). The larval season of both species partially overlap, C. maenas 527 larvae are released from May onwards and megalopae settle in the intertidal zone from the end of June 528 until the end of August (Giménez and Dirk, 2007). Interspecific competition occurs because juveniles 529 of both species develop in the intertidal zone during summer (Geburzi et al. 2018) The balance of larval 530 supply and competition of C. maenas and H. sanguineus must be evaluated considering both spring and 531 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 532 summers (temperature ~ 15 °C). 533

We hypothesise that summers characterised by long heatwaves and high temperatures due to 534 535 warming would increase performance of *H. sanguineus* larvae and exacerbate current competitive 536 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 537 temperatures are above a predefined threshold (Meehl and Tebaldi 2004; Hobday et al. 2016), can have 538 539 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 540 more frequent since the 1990's (Giménez et al. 2022). During summer heatwaves such as those 541 occurring in 2018, water temperatures around the local population reached values above 18 °C 542 (Giménez et al. 2020); temperatures in waters of the coastal Wadden Sea (where C. maenas and H. 543 544 sanguineus co-occur) were much higher (BSH, 2019).

Another important aspect considered in our analysis concerns the role of intraspecific variation 545 in performance (IVP). IVP is common in invertebrate larvae (e.g. Appelbaum et al. 2014; Spitzner et 546 547 al. 2019; Torres et al. 2020), and expected from genetic variation (Marshall et al. 2008; Durrant et al. 548 2013) or parental effects (Pond et al. 1996; Shama et al. 2014). Important IVP was found in this study 549 as variation in survival, developmental time, and growth among larvae from different females (e.g. Fig. 550 S5), which is also expressed in Figure 5 as wide ellipses. The ellipses are spread across regions where 551 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 552 combination are located. Hence, Figure 5 depicts the importance of the intraspecific variation in the 553 554 performance of the species, as opposed to what means show; the ellipses show that, for example, there 555 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 556 better than those of *H. sanguineus* at high temperatures under food limitation. Species coexistence is 557 one of the important ecological consequences of intraspecific variation (Bolnick et al. 2011; Appelbaum 558 559 et al. 2014).

560 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 561 562 short as 6 h), with variations among families; hence, H. sanguineus larvae should be able to survive 563 starvation periods as long as they can access food patches for a brief time every day. H. sanguineus 564 responds to food limitation through lengthening the development to a much smaller degree as compared 565 to C. maenas; this occurs at expenses of metamorphosing to megalopa with lower body mass. It remains 566 to be seen how such responses affect the balance of costs and benefits of metamorphosing with lower 567 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 568 569 and Giménez 2020). Under cool summer conditions, we would expect limited survival of H. sanguineus

- 570 larvae which could favour *C. maenas*. By contrast, under a warming scenario, *H. sanguineus* should
- 571 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
- 573 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
- 576 help us to understand and predict effects of warming on species replacement.
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591 used for scientific purposes.

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

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