Journal of Biogeography

WILEY

Journal of Biogeography

RESEARCH ARTICLE OPEN ACCESS

Trends in Early Larval Traits of a Global Invader at Home Across a Latitudinal Gradient: The European Shore Crab *Carcinus maenas*

Jan Phillipp Geißel[1,2] | Noé Espinosa-Novo[1,2] | Luis Giménez[2,3] | Nicole Aberle[4,5] | Gro I. van der Meeren[6] | Ralf Rautenberger[7] | Steffen Harzsch[1] | Gabriela Torres[2]

[1]Department of Cytology and Evolutionary Biology, Zoological Institute and Museum, University of Greifswald, Greifswald, Germany | [2]Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, Helgoland, Germany | [3]School of Ocean Sciences, College of Environmental Sciences and Engineering, Bangor University, Menai Bridge, UK | [4]Institute of Marine Ecosystem and Fishery Science (IMF), University of Hamburg, Hamburg, Germany | [5]Department of Biology, Trondhjem Biological Station, Norwegian University of Science and Technology (NTNU), Trondheim, Norway | [6]Institute of Marine Research (IMR), Austevoll Research Station, Storebø, Norway | [7]Division of Food Production and Society, Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway

Correspondence: Jan Phillipp Geißel (janphillipp.geissel@uni-greifswald.de)

Received: 27 January 2025 | **Revised:** 2 April 2025 | **Accepted:** 7 April 2025

Funding: This study is part of JPG's doctoral dissertation. JPG and AF were supported by the Deutsche Forschungsgemeinschaft (Research Training Group 2010: RESPONSE) at the University of Greifswald, in collaboration with the Alfred-Wegener-Institute. NE-N was supported by the Bundesministerium für Bildung und Forschung (Project MERGE; grant no. FKZ 01DN20002), Germany. FB was supported by a Deutscher Akademischer Austausch Dienst (DAAD RISE scholarship). GT and NE-N's visit to ECIMAT (Vigo, Spain) was supported through the Transnational Access ASSEMBLE+ funded by the European Union's Horizon 2020 research and innovation programme under grant agreement No 730984, 8th call (Project ROSW—PID 10370).

Keywords: intraspecific trait variation | larval body mass and performance | latitudinal multi-population study | maternal investment | phenotypic physiological plasticity | thermal tolerance

ABSTRACT

Aim: This study sets out to understand the variability in larval traits of dispersive life stages of a famous invader, the European shore crab *Carcinus maenas*, in its native distribution range.

Location: North East Atlantic coast from the Norwegian Arctic to the southern European distribution limit of *C. maenas* in Southern Spain.

Taxon: European shore crab *Carcinus maenas* (Crustacea, Decapoda).

Methods: We quantified latitudinal patterns in larval body mass, elemental composition (C and N content), and thermal tolerance of the first larval stage. We collected crabs from four populations spanning 25° of latitude (Vigo in Northern Spain; Bergen, Trondheim, and Bodø in Norway) and reanalysed published and unpublished data of body mass and elemental composition of additional populations from Germany, Wales, France, and Southern Spain. Furthermore, we used two laboratory experiments to test the thermal tolerance limits of the first larval stage from Vigo and the Norwegian populations. In the first experiment, we reared larvae from hatching to Zoea II at seven temperatures (9°C–27°C) and from hatching to LT_{50} at 6°C. In the second experiment, we exposed freshly hatched larvae acutely to increasing or decreasing temperatures (up to 40°C and down to 3°C).

Results: Across the entire European range, we found a substantial increase in dry mass and carbon and nitrogen content of freshly hatched larvae with latitude. Norwegian populations exhibited higher survival at 9°C than the Vigo population. Furthermore, LT_{50} at 6°C increased from South to North. All populations showed high survival in the range 12°C–24°C but low survival at 27°C.

Journal of Biogeography, 2025; 52:e15143
https://doi.org/10.1111/jbi.15143

Main Conclusions: Larval tolerance quantified by using survival to Zoea II is not clearly related to the tolerance quantified with the acute experiments, indicating that each method assesses different aspects of thermal tolerance. Tolerance to low temperature correlated positively to tolerance to high temperature, suggesting that variation among females in larval responses reflects a general physiological quality rather than trade-offs. We provide evidence for potentially adaptive variations in larval body mass and thermal tolerance across a latitudinal gradient for *C. maenas*.

1 | Introduction

Ocean warming, sea-ice loss, and marine heatwaves, as part of human-induced global climate change, cause major changes in marine ecosystems (Boersma et al. 2016; García Molinos et al. 2016; IPCC 2023; Poloczanska et al. 2013). Together with prevalent biological invasions, they contribute to the global reorganisation of biodiversity (Chan and Briski 2017; García Molinos et al. 2016; Gurevitch et al. 2011). The Arctic and North-East Atlantic Oceans (North, Norwegian and Barents Seas) are warming at unprecedented rates (Gerland et al. 2023; Mackenzie and Schiedek 2007; Wassmann 2011). Additionally to the general warming trend, marine heatwaves are increasing in frequency, duration, and amplitude in the world's oceans and particularly the Arctic (Huang et al. 2021; Jacobs et al. 2024; Lien et al. 2024). Range shifts, occurring across latitudinal gradients, have been correlated with temperature increases over the past decades in key species of zooplankton (Beaugrand et al. 2002, 2009), fish (Brander et al. 2003; Rutterford et al. 2023; Siwertsson et al. 2024), benthic rocky shore invertebrates (Mieszkowska et al. 2005), many NE Atlantic crustaceans (Bakke et al. 2019; Brattegard 2011; Magnússon et al. 2024), and across taxa and basins (Chust et al. 2024).

Many species of marine invertebrates, which are distributed across latitudinal gradients and experiencing current warming, develop through a complex life cycle, including planktonic larval phases. Dispersal of planktonic larvae contributes to population connectivity and larval retention to population persistence (Eckert 2003; O'Connor et al. 2007; Shanks 2009; Weersing and Toonen 2009). Larval stages are particularly susceptible to environmental drivers (Anger 2001; Pandori and Sorte 2019), but their climate vulnerability remains understudied (Pottier et al. 2022). Since larvae from different populations of a species can differ in traits such as size and tolerance to environmental drivers (Geißel et al. 2024; Storch et al. 2009), their vulnerability is likely to vary across an environmental gradient. Many key environmental factors vary across latitudinal gradients, including temperature and light, which vary seasonally, hence driving cycles of primary production and determining the quality and availability of food to larvae (Levin and Bridges 1995). Therefore, while larvae must possess traits that are adaptive to the thermal environment (e.g., thermal tolerance), they must also possess traits that are adaptive to the seasonal cycles of food availability. Across such gradients, there is a tremendous variation among larval modes of development (Byrne 2006; Levin and Bridges 1995) and larval size and body mass (Marshall et al. 2018) in marine invertebrates. Across latitudes, larval size, feeding modes, and developmental time vary in a manner that is adaptive to the cycles of food availability. For instance, the proportion of species with planktonic non-feeding larvae (or lacking a larval stage) is higher in polar regions (Marshall et al. 2018), and larvae of some species show shorter developmental times (Van Doorslaer and Stoks 2005b) and increased growth rates (Śniegula et al. 2012; Van Doorslaer and Stoks 2005a; Yamahira et al. 2007) than cogeneric species of temperate habitats (when compared at the same temperature). Shorter developmental times in populations from higher latitudes can even be observed within species with large distribution ranges (Merilä et al. 2000; Lindgren and Laurila 2010; Geißel et al. n.d.). Increased growth rates appear adaptive with increasing latitude and higher seasonality because they reduce winter mortality by producing larger body sizes and further developed phenotypes when the less productive season starts (Conover 1992). Within species, a latitudinal increase in larval body size/mass has also been documented (Landeira et al. 2017; Marco-Herrero et al. 2012; Shirley et al. 1987; Weiss et al. 2010). Those traits respond presumably to the pressures exerted by a narrow window of food availability and the low temperatures extending the larval phase towards the poles. Within species, however, temperature is a strong driver of the duration of the larval phase (Angilletta 2009; O'Connor et al. 2007) and larval size (Pettersen et al. 2019), which instead can drive the metabolic efficiency and the capacity to capture food. It is predicted that species with planktotrophic larvae will become prevalent in polar seas with ocean warming and that the duration of development will decrease substantially (Marshall and Alvarez-Noriega 2020). Larvae released with higher initial larval body mass and size usually show decreased duration of development and increased survival to moult (Emlet 1995; Levitan 2000; Oliphant and Thatje 2013). In many cases, mothers living in food-limited environments produce larger offspring, presumably as a response to food limitation or low food quality (Fox et al. 1997; George 1995; Robertson and Collin 2015). Because the developmental costs decrease with temperature, mothers from colder environments must produce larger, better-provisioned offspring that outperform smaller conspecifics (Marshall et al. 2003, 2018; Marshall and Steinberg 2014; Pettersen et al. 2019). Additionally, larvae of food-limited habitats are hatched with increased levels of lipid reserves, which can allow partial food independence during larval development (Anger 1996; Thatje et al. 2004). Overall, for marine invertebrates with complex life cycles distributed across latitudinal gradients, understanding responses to climate change requires quantification of larval traits, such as thermal tolerance and body mass, across the latitudinal distribution range.

Here, we quantified latitudinal patterns in larval body mass and reserves at hatching, and thermal tolerance of the first zoeal stage of the shore crab *Carcinus maenas*, a key predatory crab of the intertidal along the NE Atlantic coasts from Mauritania to northern Norway. Outside its wide native range, it established populations along both coasts of North America, in Patagonia, South Africa, and Australia (Behrens Yamada et al. 2005; Cohen et al. 1995; Grosholz and Ruiz 1995; Klassen and Locke 2007). *Carcinus maenas* is an opportunistic omnivorous decapod crustacean and an ecosystem engineer (Klassen and Locke 2007) with an important role in coastal food webs. In addition, *C. maenas* is a well-known invasive species, and it is regarded as one of the 100 worst invasive species by the IUCN (Lowe et al. 2000) because of the predation on native mussels, cockles, and crabs, leading to population declines and reduced catches (see Behrens Yamada 2001; Ens et al. 2022 and references therein). In Europe, the northern edge of the distribution range appears to be located between Tromsø and the North Cape (69°–71° N) in Norway (based on GBIF records and communications with Norwegian scientists). Populations are found in shallow subtidal and intertidal zones (Klassen and Locke 2007); adults mate in the intertidal, and females carry eggs and release larvae during high tides (Zeng and Naylor 1997). Larvae develop through four zoeal stages and a megalopa that settles in complex habitats of intertidal zones (Williams 1967); juveniles grow in the intertidal and eventually migrate to the subtidal in winter (Naylor 1962; Thiel and Dernedde 1994).

The pattern of distribution of *C. maenas* across latitudes follows environmental temperatures, but the physiological mechanisms are unclear, and latitudinal gradients in larval traits are likely to play a role (Compton et al. 2010; deRivera et al. 2007). In *C. maenas*, some information on the temperature sensitivity of adult traits (e.g., body size in adults correlates negatively to environmental temperature) is available (Kelley et al. 2015; Monteiro et al. 2023a). However, key information on variations in larval traits across latitudes is missing. A combination of experiments and data from the literature allowed us to quantify patterns of larval tolerance to thermal challenges from hatching to metamorphosis along the European and North American coast, including two populations in Norway (Geißel et al. n.d.). In this study, it was possible to geographically expand the data set to include a Norwegian population north of the Arctic Circle. Additionally, we quantified whether short-term acute tolerance (experiments based on temperature-ramps) would predict survival of the first Zoea under chronic exposure to thermal stress due to low or high temperatures. We also combined our data set of body mass and elemental composition of larvae at hatching with publicly available data to expand our analyses to additional *C. maenas* populations beyond the ones considered previously.

2 | Materials and Methods

2.1 | Sample Collection and Geographic Information

Berried females (female carrying eggs) of *C. maenas* (carapace width 29–60 mm) were collected from four locations spanning 25° degrees of latitude (Figure 1a). Animals from the Vigo population were collected by divers in subtidal zones next to the intertidal (< 0.5–1 m depth) of the sand bar Punta Ladeiras, in the mouth of the Miñor River, and transported to the Estación de Ciencias Mariñas de Toralla (ECIMAT) in April of 2022. At the Norwegian sites, crabs were hand-collected from underneath rocks and small boulders in the intertidal zone during low tide. To include specimens from three different sites along the latitudinal gradient along the Norwegian coastline, two sampling trips were conducted (see Table S1 for details of collection sites and times). During the first trip, females were collected from two western Norwegian populations at the Austevoll archipelago (near Bergen) and in the Trondheimsfjord (near Trondheim) in May of 2022. At Austevoll, animals were collected on beaches and rocky shores across the archipelago and held in flow-through tanks in the aquarium facilities of the Institute of Marine Research/Havforskningsinstituttet, Forskningsstasjon Austevoll. In the Trondheimsfjord, animals were collected at locations in the mid-fjord close to Trondheim and at the outer-fjord (Trondheimsleia) at Sletvik field station Norwegian University of Science and Technology (NTNU). The animals were kept in flow-through aquaria at NTNU's Trondhjem Biological Station (TBS). Animals from the northernmost station in Norway (Bodø) were collected at the beaches of Skivika and Ausvika and south of Saltstraumen in June of 2022 and maintained in flow-through water tanks at NIBIO's laboratory in Bodø. Until the transport to the Biologische Anstalt Helgond (BAH) at the Alfred Wegener Institute (Alfred-Wegener-Institut Helmholtz-Zentrum für Polar-und Meeresforschung 2023) on Helgoland, Germany, all berried females were kept in flow-through tanks with natural seawater at ambient temperature and salinity from each collection site at the time of collection (Vigo: salinity 21.5–25.5 PSU & temperature 12.6°C–14.6°C, Bergen: 30.2–31.8 PSU & 11.2°C–12.7°C, Trondheim: 19.9–29.4 PSU & 11.6°C–12.2°C, and Bodø: 30.0–30.4 PSU & 10.3°C–13.9°C). For the transport to Germany, animals were placed in individual plastic containers (1 L), partially filled with seawater from the respective collection sites and a wet towel. The containers were then placed in a Coleman cooler box to ensure constant temperatures during transportation. Also, additional water from each collection site was transported in the cooler and was used for seawater exchange halfway through the transport (transport duration less than 48 h). Experiments were then performed at the BAH.

The seasonal range of average monthly sea surface temperatures of the chosen sites is as follows: Vigo, 12°C–19°C; Bergen, 2°C–16°C; Trondheim, 3°C–15°C; Bodø, 2.5°C–15°C for the 10 years from 2011 to 2022 (see Figure 1b, generated using E.U. Copernicus Marine Service Information; https://doi.org/10.48670/moi-00165). The water temperatures measured in Bodø (10°C–14°C) at the time of collection were extraordinarily high for the region as collection time coincided with a heatwave with record high air temperatures for that summer (Copernicus Climate Change Service/ECMWF 2022). On a local scale, there are differences between the three Norwegian locations. The site in the Bergen region (the Austevoll archipelago) is more directly exposed to the North Sea, and thus, seawater is saltier and cooler than in the actual Bergen area. Water exchange in Trondheimsfjord occurs via surface inflow from the Norwegian Current, a branch of the North Atlantic Current, and seawater temperatures within the fjord are typically warmer than at the coasts of the Norwegian Sea. Bodø was the only site north of the Arctic Circle and thus is usually exposed to colder water temperatures.

2.2 | Larval Traits

Freshly hatched larvae from each female were divided into two groups: The first group was used for quantification of

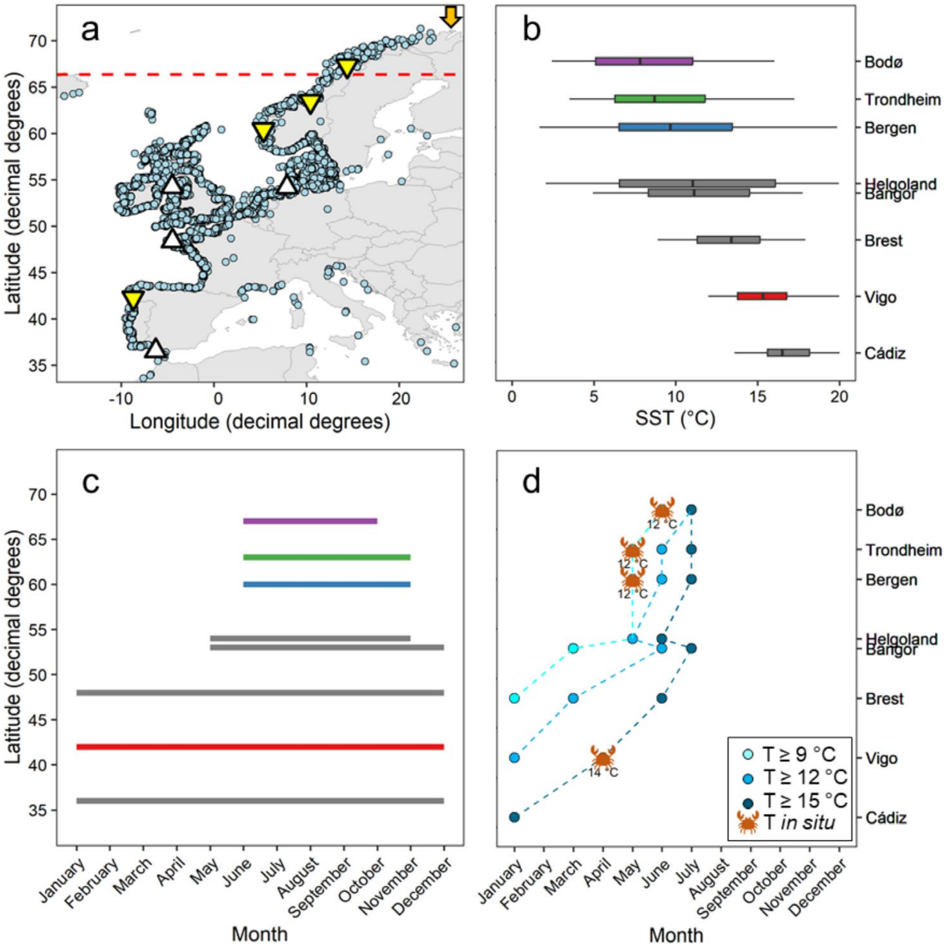


FIGURE 1 | (a) Map illustrating the distribution range and collection sites of the shore crab *Carcinus maenas* along the European Atlantic coast (Mercator projection). Sighting records from GBIF (GBIF 2023) are shown by light blue points, collection sites in this study are shown in downward yellow triangles. Sites for literature data are shown in upward white triangles, the red dashed line indicates the Arctic circle at 66°33′ N, and the orange arrow indicates the estimated northern edge of *C. maenas* distribution. (b) Boxplots of yearly sea surface temperatures (SST) in °C for the investigated sites. (c) Months with average monthly SST > 9°C for all studied sites. (d) Circles indicate the average first month of the year with SST reaching threshold temperatures for each site: Light blue (≥ 9°C), medium blue (≥ 12°C), and dark blue (≥ 15°C). Crab symbols indicate the collection month of the respective population and are associated with the average temperature measured in the intertidal at collection. All SSTs based on ten years of daily averaged SST (Generated using E.U. Copernicus Marine Service Information; https://doi.org/10.48670/moi-00165). In (b) and (c): Sites with data obtained in this study are represented in red (Vigo), blue (Bergen), green (Trondheim), and purple (Bodø); sites with data from previous publications are represented in grey.

body mass and elemental composition (carbon and nitrogen content), and the second group was used to estimate thermal tolerance.

Freshly hatched Zoea I (for each female: 5 replicates of 50 larvae each) were randomly sampled to determine dry mass (DW), carbon (C), and nitrogen (N) content. In crustaceans, the larval carbon content is considered a proxy for lipid reserves (which are very sensitive to environmental fluctuations/variations), while the nitrogen content is used as a proxy for the protein content (Anger 1998; Anger and Harms 1990; Dawirs 1986; Dawirs et al. 1986). Hence, the C:N ratio is a good indicator of allocation of reserves (Anger and Harms 1990). When possible, these measurements were conducted for additional hatches (see Table S2 for an overview). Larvae were rinsed with distilled water, gently blotted dry with fluff-free tissue, placed in a pre-weighed tin cartridge, and stored at −20°C for further analysis. To determine the dry mass, samples were freeze-dried for 48 h (Christ Alpha 1–4 freeze-drier) and consecutively weighed using a microbalance (microbalance, Sartorius MCA2.7S-2S00-M, precision 1 μg). Carbon and nitrogen contents were determined using an elemental analyser (Vario MICRO cube CHNS analyser, Elementar Analysensysteme).

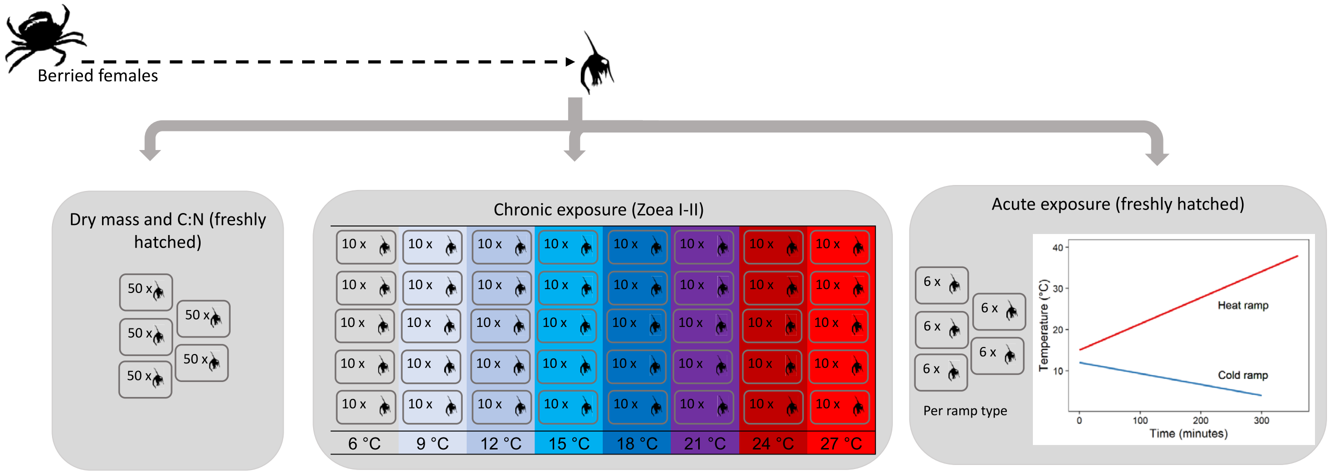
Additional data on freshly hatched larvae across the European Atlantic coast were obtained from literature data (Anger et al. 1998; Anger and Harms 1990; Dawirs 1980, 1982, 1986, 1987; Harms et al. 1994; Šargač et al. 2021, 2022; Spitzner et al. 2019; Torres et al. 2020) and from Geißel et al. (n.d.) as well as unpublished own data (see Table S2). Data were included only when hatching and embryogenesis occurred in seawater (salinity ≥ 30 PSU) and only if hatching occurred in spring–summer. If data from the literature did not report whether the larvae used for the biomass determinations originated from one or more females, data were used as if originating from only one female.

Thermal tolerance of Zoea I was quantified using two approaches: (1) chronic exposure, that is, freshly hatched Zoea I were reared under constant temperature until they died or moulted to Zoea II, and (2) acute exposure, that is, freshly hatched Zoea I were exposed to temperature ramps of increasing or decreasing temperatures within 12 h. Thermal ramps allow the estimate of critical thermal limits (Rezende et al. 2020). This parameter provides insights into the temperature ranges in which animals can remain active while under acute exposure (Somero 2005). Furthermore, Rezende et al. (2014) showed that there might be a trade-off between tolerances to chronic and acute exposure.

Before hatching, females were maintained individually in 5 L aquaria in UV-treated and filtered (mesh size: 2 μm) natural seawater (33 ± 1 PSU) at the temperature of each site at the time of collection (Vigo: 15°C, and Norwegian populations: 12°C). Females were fed twice a week with frozen shrimps (*Crangon crangon*), and water was changed daily to ensure high water quality at the time of hatching. At hatching, larvae were transferred into the experimental units.

For the chronic exposure experiments, survival and duration of development were determined when larvae were reared at constant temperatures until they reached Zoea II. The experiments were conducted in temperature-controlled rooms (± 1°C) with a 12:12 h light:dark cycle. Larvae were assigned randomly to one of the experimental temperatures: 6°C, 9°C, 12°C, 15°C, 18°C, 21°C, 24°C, and 27°C (Figure 2). Each treatment comprised five replicates of 10 larvae each, reared in 60 mL glass beakers. This design allowed the evaluation of the combined effect of population and female of origin and temperature during the development of the Zoea I. The experimental temperatures were chosen to match the span of conditions the larvae could experience in their respective environments and covering critical extremes. Experiments were conducted with larvae from each female of origin (i.e., 20 hatches originated from 20 females; six from Vigo, five from Trondheim, four from Bergen, and five from Bodø). Larval rearing was performed following standard rearing techniques (Torres et al. 2021). Water and *ad libitum* food (freshly hatched *Artemia* sp. nauplii—Great Salt Lake Artemia) were changed daily. During the daily water change, survival and moulting were monitored, and exuviae and dead larvae were discarded.

For the acute exposure experiments, larvae were exposed to thermal ramps in programmable incubators (GES-E230 Keimschrank with RUMED CONTROL2015 touch, Rubarth Apparate GmbH) for up to 12 h. The heat ramps were programmed to temperature increases of 4°C per hour until reaching 40°C, and the cold ramps were set to decrease temperature by 3°C per hour until reaching 3°C. The ramps were conducted within 12 h of hatching and consisted of five replicates of six freshly hatched larvae per female of origin. At hatching, individual larvae were randomly placed in individual wells in six-well plates (Corning Incorporated costar polystyrene cell culture plates). Each well (10 mL) was filled with seawater at the hatching temperature without food. The six-well plates were placed on trays and left partially covered with lids to reduce water loss and increases in salinity due to evaporation. Ramps were conducted for most of the hatches used in the chronic exposure experiment and additional hatches: three from Vigo, three from Bergen, three from Trondheim and nine from Bodø. The larvae of each hatch (five six-well plates with six individual larvae each) were exposed to a heat ramp and the same number to a cold ramp at the same time. Every 30 min, each larva was inspected twice, and temperature was measured and recorded. If a larva was lying at the



Latitude	67 °N	63 °N	60 °N	42 °N
Site	Bodø	Trondheim	Bergen	Vigo
Females	10	6	14	19

Latitude	67 °N	63 °N	60 °N	42 °N
Site	Bodø	Trondheim	Bergen	Vigo
Females	5	5	4	6

Latitude	67 °N	63 °N	60 °N	42 °N
Site	Bodø	Trondheim	Bergen	Vigo
Females	9	3	3	3

FIGURE 2 | Experimental design to study the responses of *Carcinus maenas* larvae from four different populations: Vigo (Spain), Bergen, Trondheim, and Bodø (Norway), to different temperature conditions. Dry mass, and carbon (C) and nitrogen (N) contents were determined for five replicates of 50 larvae each for each female of origin. For the chronic exposure, larvae were reared from hatching to Zoea II at seven constant different temperatures: 9°C, 12°C, 15°C, 18°C, 21°C, 24°C, and 27°C, at 6°C larvae were reared from hatching until LT_{50} was reached, represented from light grey (6°C) to red (27°C). Larvae were reared in five replicates of ten individuals each. Experiments were repeated for larvae originating from each female. For the acute exposure, larvae were exposed to heat and cold ramps. Temperature-ramp experiments were conducted with five replicates of six individuals per hatch per ramp.

bottom of the six-well tray without movement in both visual inspections, it was assumed to be in a heat knockdown/chill coma and was counted as dead and thus removed from the experiment. Because constant monitoring was not possible but visual inspections occurred in intervals, a temperature datum was generated when a larva was last seen alive and a second temperature datum when it was first seen knocked down. Based on those two values, we calculated an average temperature of knockdown/chill coma (i.e., death).

2.3 | Data Analysis

Survival in the chronic experiment was calculated as the proportion of larvae surviving from hatching to Zoea II. To avoid situations of log(0) values, data were transformed using the formula $p' = [p(N-1)+0.5]/N$, where N is the number of larvae in the respective replicate, that is, 10. The proportional survival was then transformed into logarithmic and logistic scales. Duration of development was defined as time (days) from hatching to moult to Zoea II. Since survival was consistently low in the 6°C treatment, the LT_{50} (average time until mortality exceeds 50%) was calculated discriminated by female of origin as a way to assess the tolerance to cold. For the duration of development, additional models were constructed using inverse temperature polynomials of 2nd and 3rd degree.

Data analysis was performed using R version 4.3.2 (R Core Team 2022). Means and standard errors were calculated using the package "plyr" (Wickham 2011). The combined effects of temperature and population of origin were quantified using mixed modelling (Zuur et al. 2009), with survival and duration of development as response variables. The models consisted of temperature and population of origin as fixed factors and female as a random factor. Model analysis was performed by applying backward model selection (Zuur et al. 2009) based on the second-order Akaike information criterion (AICc). The package "nmle" (function lme and gls, Pinheiro et al. 2019) was used for model fitting with generalised least squares. Model selection was performed stepwise: (1) The random terms were compared through restricted maximum likelihood (REML), and (2) the fixed terms were compared through maximum likelihood, after refitting the model with the best random structure. The model with the lowest AICc was selected. For LT_{50}, generalised least squares were used. Plots were created using "ggplot2" (Wickham 2016) and maps using "rworldmap" (South 2011).

We also tested if the incubation times of berried females in the laboratory affected our results. We used Pearson correlation between incubation time and larval traits averaged by females of origin. We did not find any evidence of such effects (correlations were not significant); therefore, we did not consider incubation times as a response variable in data analysis (see Table S3). Similarly, we conducted correlation analysis to investigate the potential effects of the size of females (carapace width, CW) on the dry mass of freshly hatched larvae or their performance, but no correlation was significant (Table S4). p-values < 0.05 were considered statistically significant. All data for this paper will be available from DRYAD (https://doi.org/10.5061/dryad.hdr7sqvtw).

3 | Results

For simplicity, we use the term "Vigo population" for larvae obtained from Vigo, Spain, and similarly for the Norwegian sites. This does not imply that these organisms represent the whole respective coasts. Similarly, we refer to the organisms from one collection site as local populations, without inferring that these "populations" are genetically separated or distinctive in terms of population connectivity; for example, connection through larval dispersal could be possible.

3.1 | Dry Mass and Elemental Composition

There was a clear positive correlation between latitude and dry mass of freshly hatched larvae (Figure 3a). The mean dry mass of Zoea I varied between $8.9 \pm 0.2\,\mu g\,ind^{-1}$ (mean ± SE) and $9.16 \pm 0.3\,\mu g\,ind^{-1}$ (in larvae from Vigo and Cádiz, respectively) at the southern end of the European distribution range (Figure 3a) and $11.96 \pm 0.4\,\mu g\,ind^{-1}$ in larvae from the Arctic population, Bodø at the northern end, with all Norwegian populations showing average dry mass $> 10\,\mu g\,ind^{-1}$ (see Table S4). The best model (General least squares) retained the population as a fixed effect ($\Delta AICc = 8$). Additionally, we found considerable intra-population variation in the average dry mass among larvae from different females. For Helgoland (German Bight: 54° N), we had data available from different years of collection (1980–2019), but such data did not show evidence of a temporal trend (the best model did not contain "year", $\Delta AICc = 14$ lower than the model with "year"). Larval C:N ratios varied considerably across latitudes but without evidence of a latitudinal trend (Figure 3b; best model did not retain latitude $\Delta AICc = 9$ against a model with latitude, Table S5).

3.2 | Thermal Performance: Chronic Exposure

Larval survival to Zoea II depended on temperature and varied among females (Figure 4, Table S9: best model retained population and temperature in the fixed structure). In all populations, survival was consistently low at 6°C; hence, we resorted to measuring LT_{50}, and we found a strong increase in LT_{50} with latitude (Figure 5). There was some variation in survival among populations, in the range of 9°C–27°C, but it was partly overridden by the variability among larvae from different females (Figure 4: note error bars). In the lower temperature range (≤ 15°C), survival increased with temperature and reached optimal values in the range 15°C–21°C. In the higher temperature range, low survival rates were recorded at 27°C for all four populations (Figure 4). Larvae from the northernmost population (Bodø) showed the highest survival of all populations in all temperatures > 12°C.

Since at 6°C, only very few larvae survived to Zoea II ($\leq 4\%$), we used an approach comparable to LT_{50} (median lethal time of exposure) to analyse variation in the endurance to low temperature until mortality exceeded 50% (Figure 5). We found evidence of increased tolerance to 6°C with latitude (best model retained latitude: $\Delta AICc = 6$ against a model without latitude). In larvae from Vigo (Spain), average mortality exceeded 50%

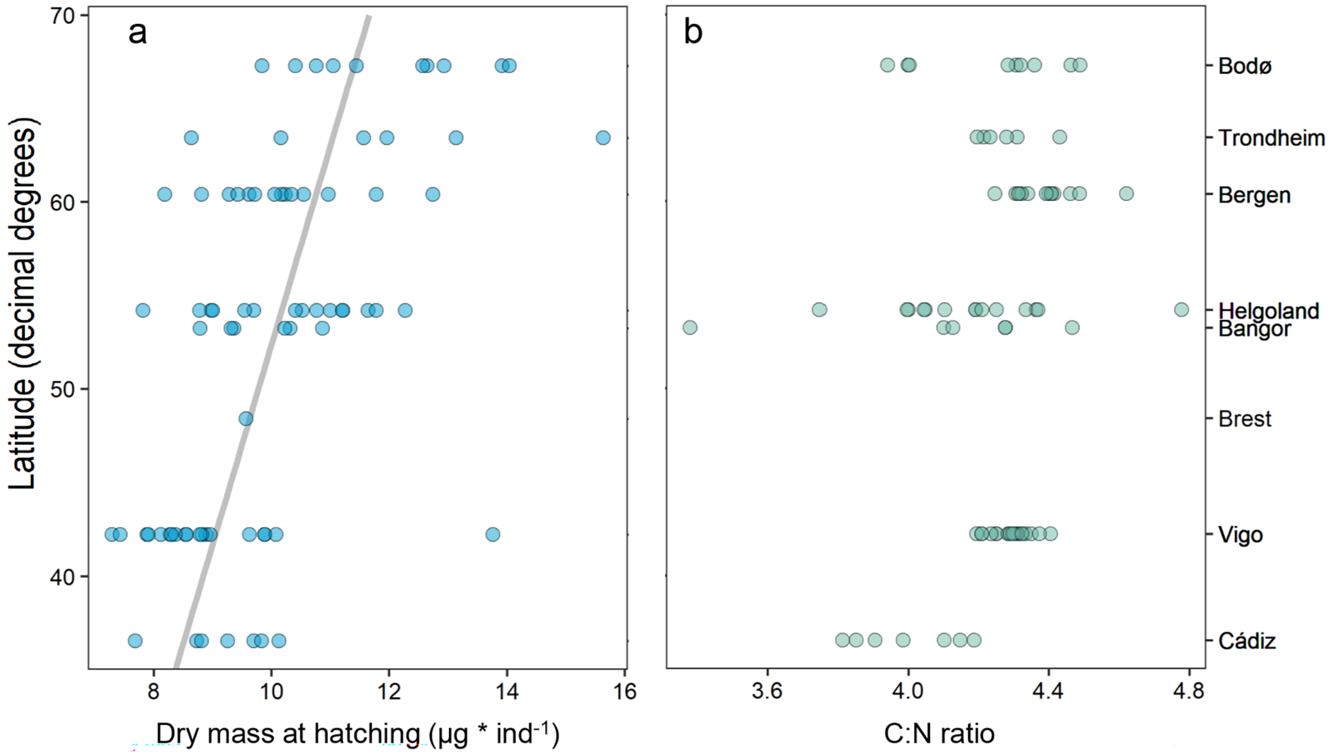


FIGURE 3 | (a) Dry mass at hatching for larvae of *Carcinus maenas* discriminated by population of origin (µg ind^{-1}). (b) Ratio of carbon to nitrogen content (C:N) at hatching discriminated by population. The left *y*-axis shows latitude (decimal degrees) and the right *y*-axis shows the site names. Data shown as means per female of each population. Data were included only when hatching and embryogenesis occurred in seawater (salinity ≥ 30 PSU) and only with spring–summer hatches. The grey line indicates the best model fit (general least squares).

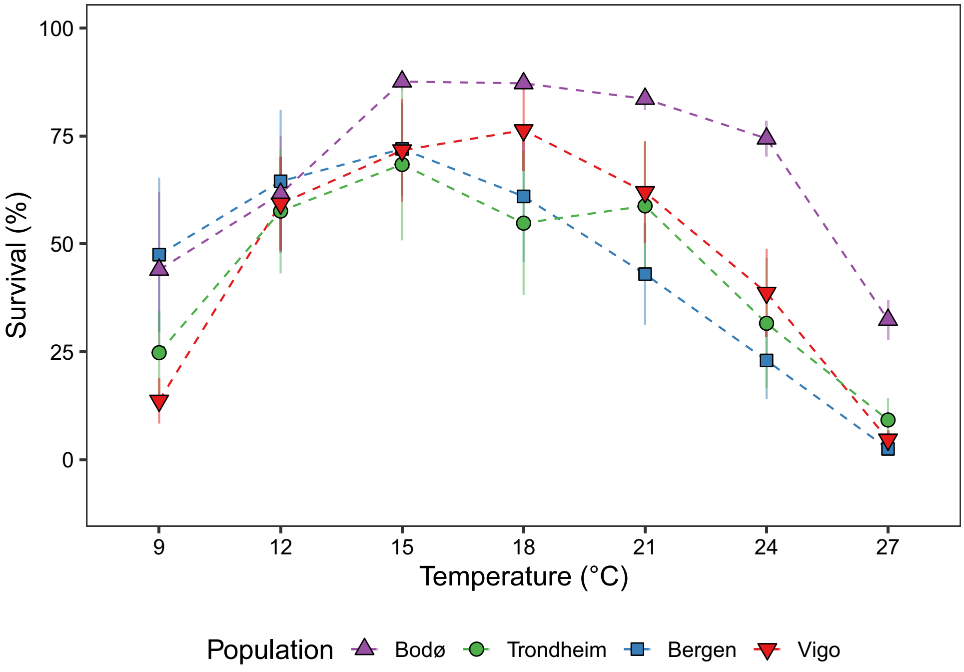


FIGURE 4 | Average survival to Zoea II (%) for larvae of *Carcinus maenas* discriminated by temperature (9°C, 12°C, 15°C, 18°C, 21°C, 24°C, and 27°C) for larvae originating from females of four populations (Vigo = 6, Bergen = 4, and Trondheim = 5, and Bodø = 5). Data presented as mean values ± SE of larvae produced by each female of origin. Symbols represent larvae originating from females from different populations (purple upward triangles: Bodø, green circles: Trondheim, blue squares: Bergen, and red downward triangles: Vigo).

after 14.2 days; in larvae from western Norway after 22.3 days for Bergen and 19.2 days for Trondheim, and in the Arctic population from Bodø, 34.7 days.

The duration of development (in days) decreased with increasing temperature in a non-linear pattern; the best models retained the interaction of temperature and population in the fixed term

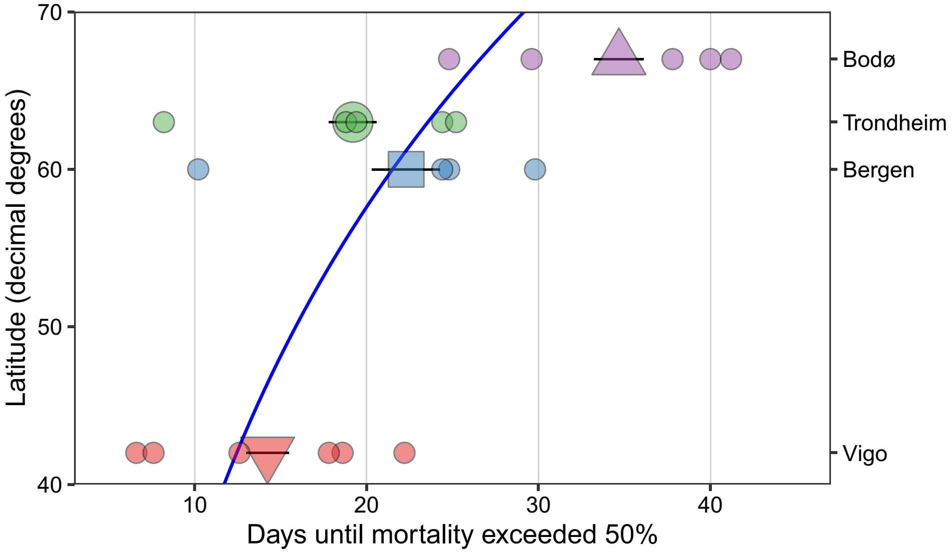


FIGURE 5 | LT$_{50}$ for Zoea I larvae of *Carcinus maenas* exposed to 6°C. The *x*-axis shows the mean time until mortality exceeded 50% discriminated by population (right y-axis). Large symbols represent the mean of the variation of the four to six females per population, with error bars indicating SE, (red downward triangles: Vigo, blue squares: Bergen, green circles: Trondheim, purple upward triangles: Bodø), small circles indicate the mean per female. The blue line indicates the generalised linear mixed model (GLMM).

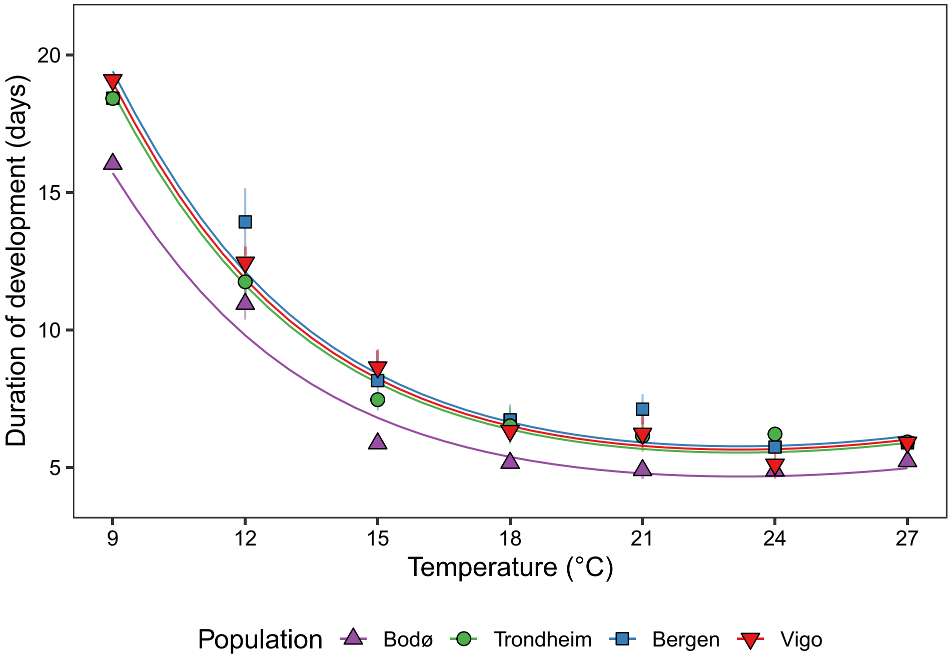


FIGURE 6 | Duration of development (days) from hatching to Zoea II discriminated by temperature (°C) for larvae of *Carcinus maenas*. Data shown as mean values ± SE. Lines indicate predictions based on the best model (3rd-degree polynomial). Symbols as in Figure 4.

when temperature was treated as a factor (Tables S6–S8). The best model was a 3rd-degree polynomial, retaining population in the fixed part; larvae from Bodø developed significantly faster than those from other populations (Figure 6). At 9°C, the average duration of development to Zoea II was >15 days for all populations. At 15°C, it decreased to below 10 days for all populations and 5 to 7 days at 18°C. The northern populations showed a tendency to reduce the duration of development compared to the more southern populations, especially at low temperatures (<18°C), with the northernmost population (Bodø) developing significantly faster at all temperatures than the other three populations.

3.3 | Thermal Performance: Acute Exposure

During the heat ramps, there were no survivors at the ramp's endpoint temperature, that is, all larvae reached the knockdown temperature before reaching 40°C. The maximum knockdown temperature (i.e., average temperature at which 50% of the

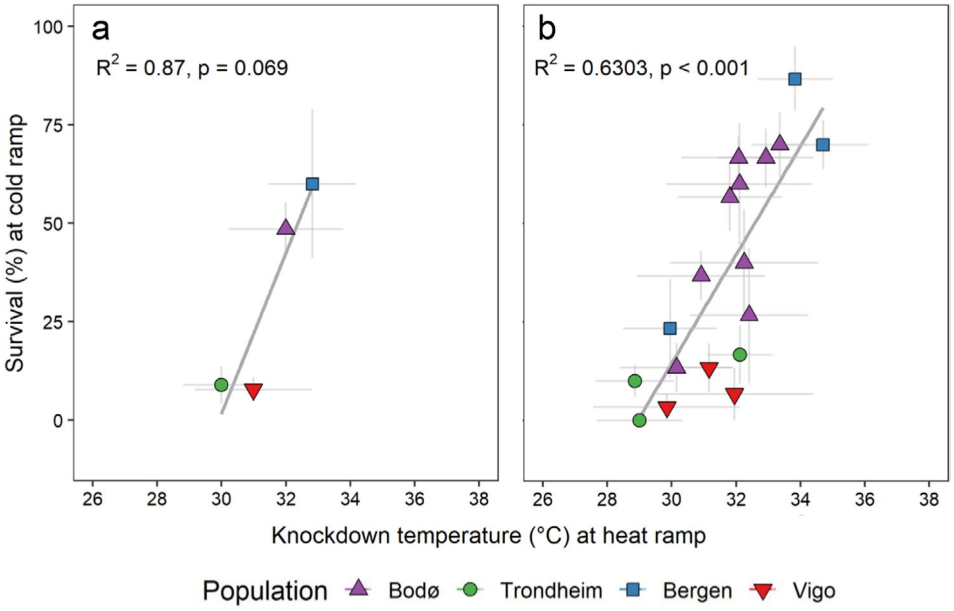


FIGURE 7 | Integrated responses of average temperature (°C) of heat knockdown during exposure to a heat ramp (temperature on the *x*-axis) vs. survival during exposure to the cold ramp (percentage of survival at 3°C on the *y*-axis). Larvae of *Carcinus maenas* originated from females of four populations: Vigo (*n* = 3), Bergen (*n* = 3), Trondheim (*n* = 3), and Bodø (*n* = 9). Data presented as mean values ± SE of the temperature of the last observation before knockdown and first observation after knockdown for (a) all females of each population and (b) discriminated by each individual female of origin for each population. Symbols as in Figure 4. Grey lines indicate the correlation between heat knockdown temperature during exposure to a heat ramp and the percentage of survival during exposure to the cold ramp.

larvae were immobilised/killed by heat) varied between populations between 29.9°C ± 1.2°C (Trondheim) and 32.8°C ± 1.3°C (Bergen). The highest temperature the ramps reached before knockdown was 36°C (larvae from the Bergen population). The best model describing the response did retain population in the fixed part, but the AICc < 3 against the null model, providing limited evidence for population-level effects (Table S10). Therefore, potential differences among populations seem to be overridden by the high variation within each population (see error bars in Figure 7a).

When exposed to the cold ramps, a large proportion of larvae were able to reach the endpoint of the ramp (3°C) without reaching the chill coma. Therefore, we quantified tolerance through the percentage of survivors, that is, larvae that did not reach the chill coma at the ramp's endpoint temperature (i.e., 3°C). The percentage of survivors varied between 7.8% ± 2.9% for Vigo and 60.0% ± 18.9% for Bergen with no apparent latitudinal trend, but the best model retained population in the fixed part (ΔAICc = 8 against a model without population).

The two populations (Bodø and Bergen) that had the highest tolerance to increased temperature (highest upper knockdown temperature, Figure 7) also had the highest tolerance to low temperature (highest survival after the exposure to the cold ramp, Figure 7); here, responses were not significantly correlated (Figure 7a) due to important variation in performance among larvae from different females (see Figure 7b: larvae from Bergen population). However, females producing larvae with high tolerance to increased temperature also produced larvae with high tolerance to low temperature (Figure 7b: positive significant correlation).

3.4 | Relationships Among Larval Traits

We did not find evidence of a relationship (i.e., no significant correlation) between the performance of larvae in the acute exposure experiments (heat knockdown and chill coma temperatures) and the lowest and highest tolerance temperatures in the chronic exposure experiments. Larvae of females that showed high heat knockdown temperatures in the heat ramp did not necessarily have siblings that showed high survival in 24°C and 27°C under chronic exposure. Similarly, survivor proportions in the cold ramp did not correlate with the survivor proportion in the two lowest temperatures (9°C and 12°C) under chronic exposure (Table 1).

There were no significant correlations between survival and duration of development under chronic exposure to temperature and dry mass at hatching (Table 2). The correlation coefficients of the interactions were small for all tested temperatures (Figure 8a,b).

4 | Discussion

This is the first study quantifying early larval traits across the European coast (Northern Norway to Southern Spain), i.e., most of the native range of the global invader *Carcinus maenas*. We found a substantial increase in body mass of freshly hatched larvae with latitude across the European native distribution range; across the gradient, larvae hatched with comparable proportions of carbon and nitrogen. The acute thermal tolerance range of *C. maenas*, defined from knockdown/chill coma temperatures, ranged between below 3°C at the lower end and 29°C–33°C at the upper end, showing that the range in larval thermal tolerance (already in the first larval stage) is narrower than the range in adults (e.g., for adults, the lower thermal limit is below 0°C and upper thermal limits are at 35°C–37°C (Tepolt and Somero 2014)). This highlights that larvae generally have narrower tolerance windows than adults, which can be regarded as an important bottleneck in a population's ability to persist (Pandori and Sorte 2019; Sanford et al. 2006). Larvae from females collected near the northern range edge of distribution developed significantly faster (in $T > 6$°C) and showed higher tolerance to low temperatures (longer LT_{50} at 6°C) and higher survival rates ($T \geq 12$°C) than those from collection sites in southern Norway and Spain. The Norwegian populations showed higher survival to Zoea II at 9°C than that from Vigo, Spain. However, we also found strong variation in survival among larvae from different females within all populations. Under acute exposure to high/low temperatures, we found that siblings tended to perform well both in the cold and heat ramps or in neither, indicating that their responses reflected a general physiological quality rather than trade-offs. High performance under acute exposure to high/low temperatures did not translate into high performance under chronic temperature exposure. We discuss these patterns and their implications in detail and evaluate our results in the contexts of intraspecific variability of a species with a wide distribution range, macrophysiology, and invasion biology.

TABLE 1 | Correlation coefficients, R^2, and p-values for the relationships between survival (%) in the two coldest and two warmest temperatures (°C) that permitted survival in the chronic exposure experiment tested vs. the performance in the cold ramp (survival % at the end of ramp) and heat ramp (heat knockdown temperature) for larvae of *Carcinus maenas*, respectively. Values are based on means by females.

Survival	Ramp type	Correlation coefficient	R^2	p
9°C	Ramp down, survival (%)	0.4725	0.2233	0.1679
12°C	Ramp down, survival (%)	0.0331	0.0011	0.9276
24°C	Ramp up, LT_{50}	0.0385	0.0015	0.9159
27°C	Ramp up, LT_{50}	−0.1473	0.0217	0.6846

4.1 | Larval Body Mass Increases With Latitude

Body mass of freshly hatched larvae of *C. maenas* increased from South to North while proportions of carbon and nitrogen were comparable across populations. Increased maternal investment has been found in other crab species that produce larger offspring, higher brood weight, or shifts from income to capital breeding in higher latitudes (Baldanzi et al. 2018; Landeira et al. 2017; Marco-Herrero et al. 2012; Reese et al. 2024; Shirley et al. 1987; Weiss et al. 2010). The inverse relationship between latitude and larval size is attributed to field temperature in Decapoda with pelagic larvae (Lindley 1998). Offspring size tends to increase with latitude in many invertebrate, fish, and amphibian taxa (Marshall et al. 2018). In our study, the increased body mass with latitude would appear adaptive since animals from populations with higher larval body mass showed longer cold endurance at 6°C. However, there was no significant correlation between survival under chronic exposure and duration of development with dry mass at hatching. In any case, increased body size at hatching may be an adaptive response to potentially increased food limitation in the colder temperatures at higher latitudes. As a follow-up to this study, it would be

TABLE 2 | Correlation coefficients, R^2, and p-values for the relationships between survival under chronic exposure to temperature and duration of development vs. the mean dry mass at hatching for larvae of *Carcinus maenas*, respectively. Values are based on means discriminated by females.

Response	Temperature (°C)	Correlation coefficient	R^2	p
Survival vs. dry mass at hatching	9	−0.0056	0.0000	0.98
	12	−0.2001	0.0401	0.41
	15	−0.0450	0.0020	0.85
	18	−0.0819	0.0067	0.74
	21	0.1323	0.0175	0.59
	24	0.1017	0.0103	0.68
	27	0.1423	0.0203	0.56
Duration of development vs. dry mass at hatching	9	−0.3192	0.1019	0.29
	12	−0.2245	0.0504	0.36
	15	−0.4355	0.1897	0.07
	18	−0.2684	0.0720	0.27
	21	−0.2593	0.0672	0.28
	24	0.2996	0.0898	0.24
	27	−0.3926	0.1541	0.17

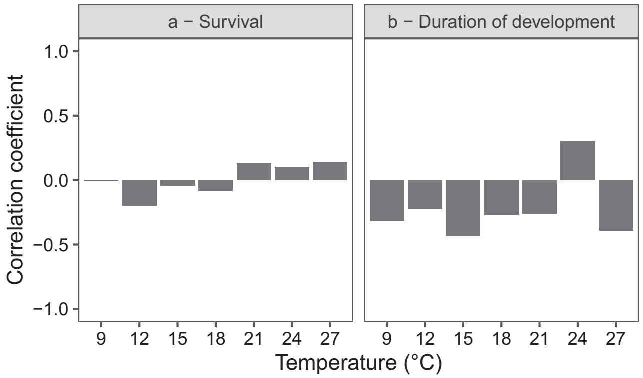


FIGURE 8 | Correlation coefficients: between (a) survival or (b) duration of development and dry mass at hatching under chronic exposure to temperature (°C) for larvae of *Carcinus maenas*.

highly valuable to investigate whether such a gradient in dry mass can also be observed in non-native populations. Understanding whether non-native populations exhibit larval body mass variations aligned with their respective latitude or their population of origin could provide crucial insights into whether these patterns are driven by adaptation or plasticity.

A potential source of variation in offspring size is associated with female size. In marine invertebrate species, offspring size is highly variable (Marshall and Keough 2007) and positively correlated with the mother's size across phyla, including crustaceans (Clarke 1993; Glazier 1992; Rollinson and Rowe 2016; Sakai and Harada 2001). Such a trend occurs presumably as an adaptive mechanism (Rollinson and Rowe 2016); for example, higher investment per larva can accelerate development (Oliphant and Thatje 2013). However, for *C. maenas*, we did not find evidence of a relationship between female size (carapace width, CW) and dry mass or carbon content at hatching (see Table S3); furthermore, such a relationship is not found consistently among decapod crustaceans (Giménez 2020). Variation in body mass at hatching can be driven by environmental conditions experienced by embryos (González-Ortegón and Giménez 2014; Šargač et al. 2022; Torres et al. 2020). Overall, the latitudinal trend found here appears to be unrelated to variations in female size, but it may reflect either latitudinal variations in maternal conditions or local adaptations.

4.2 | Larval Thermal Performance Varies Between Populations of *C. maenas*

An important question was to determine if females from the northern populations produced larvae that were particularly tolerant to low temperatures. Cold tolerance usually increases with latitude at the interspecific level (Sunday et al. 2019) and within species (Gaitán-Espitia et al. 2014, 2017). For *C. maenas*, such tolerance would enable larvae to hatch at lower temperatures and then extend the season of larval release. The experiments of chronic exposure showed that Norwegian populations had higher survival to Zoea II at 9°C. With an increasing latitude of origin, larvae of *C. maenas* showed the ability to persist longer at 6°C, with LT_{50} more than doubling from Spain to the Arctic. However, acute exposure experiments did not provide evidence of increased tolerance to low temperatures. If any, the evidence of increased tolerance to low temperature in northern populations is limited, at least for the range studied here. Perhaps, a population located even closer to the poleward distribution range edge or an offshore population from Iceland or the Faroe Islands could show increased tolerance towards lower temperature; in particular, those located offshore appear genetically distinct (i.e., form clade of three exclusive haplotypes) from those so far recorded on the continental-shelf in Europe (Roman and Palumbi 2004). The absence of cold tolerance found in this study could also result from a strong homogenising gene flow from core populations to the range edge or be caused by other adaptations that mitigate exposure to temperature extremes (Pallarés et al. 2024).

Further, we wanted to determine the tolerance to high temperatures and whether tolerance to low temperatures correlated negatively with tolerance to high temperatures. Tolerance to high temperatures can have important consequences in light of the increased frequency of marine heatwaves occurring along the distribution range (Giménez et al. 2024; Madeira et al. 2012; Monteiro et al. 2023b). We found unexpectedly high tolerance to temperatures as high as 24°C in the northern populations where heatwaves are becoming more common; indeed, marine heatwaves are of similar intensities or stronger in the Arctic compared to other ocean basins, and their annual intensity, frequency, and duration have increased substantially over the last decades (Huang et al. 2021). Marine heatwaves contribute to the decline of coastal foundation species (Smith et al. 2024). These effects are typically most pronounced closer to the warm-range edge of a species (Smith et al. 2024). While *C. maenas* will be challenged by long-term warming and increasing marine heatwaves at the southern end of its distribution range (Monteiro et al. 2023b; Souza et al. 2022), warming scenarios might prove beneficial for northernmost populations when compared to more warm-sensitive boreal and Arctic species. Fluctuations in habitat temperature were shown to have strong effects on populations; in the invasive range in North America, exceptionally warm summers, as well as particularly cold winters, springs, and summers, resulted in reduced numbers of *C. maenas* in the intertidal in the following year (Quinn 2018). In addition, unusually warm years allowed for poleward range expansions that persisted over years (Behrens Yamada et al. 2017, 2021). The high tolerance to high temperatures could indicate a potential trade-off in physiological responses, but tolerance to low and high temperatures was positively correlated. Such correlation suggests overall variations in larval physiological quality whereby females providing larvae that are better at tolerating low temperatures are also better at tolerating high temperatures.

Another important point was that experiments of acute and chronic exposure appear to highlight different aspects of thermal tolerance. For some species, it appears possible to conceptually unify different measures of thermal physiology (Cooper et al. 2008), but this does not seem to be the case for *C. maenas*. Hence, here, chronic exposure experiments seem to be the best option because it can be determined whether larvae actually survive events of extreme temperatures as would be the case during heatwave events. It has been suggested that there is a trade-off between a species' critical thermal maximum (CT_{max}) and thermal susceptibility, that is, the sensitivity to temperature change, defined as the rate of decay in tolerance (e.g., survival) with the duration of an ongoing heat challenge. This might be why even strong eurytherm species do not exhibit high CT_{max} and a low thermal susceptibility at the same time but only one of the two (Rezende et al. 2014). Based on our comparison of the performance under chronic vs. acute exposure to high temperatures, this might also be the case for Zoea I larvae of *C. maenas*: that is, high knockdown temperatures (low thermal susceptibility) during acute exposure do not translate into higher survival rates under high temperatures during chronic exposure (high CT_{max}).

Overall, the lower mean annual and summer seawater temperatures (Figure 1b) would match the slightly elevated cold temperature tolerance found for larvae from the Norwegian populations. It can be speculated that populations located even further north would show increased cold tolerance. On the other hand, the tolerance to high temperatures found across the full range studied could provide larvae with some capacity to tolerate heatwave events during early development. Concerning currently observed poleward range expansions (Behrens Yamada et al. 2017; Magnússon et al. 2024; Roman 2006; Yorio et al. 2020), increased larval body mass at hatching with increasing latitudes may provide an advantage towards the poles, but the potential effect of increased thermal tolerance appears to be limited. Since there is currently no knowledge of the genetic variation of *C. maenas* populations north of Trondheim (Roman and Palumbi 2004), genotypes found in introduced populations which originate from northern Norway would not be attributed to their origin in population genetic surveys in the invasive ranges. Especially in the presence of genotypes recovered in North America that cannot be attributed to populations in the native range (Roman 2006), this knowledge gap should be filled urgently to better understand ongoing range expansions and attribute invasions to their population of origin (Haubrock et al. 2024).

Author Contributions

J.P.G., N.E.-N., G.T., L.G., and S.H. contributed to the conception and design of the study. J.P.G., N.E.-N., G.T., and L.G. obtained the experimental females. J.P.G. and N.E.-N. performed the experiments. J.P.G. and L.G. analysed the data. The first draft of the manuscript was written by J.P.G. All authors discussed the results, contributed critically to the drafts, and gave final approval for publication.

Acknowledgements

We would like to thank the technical staff from the ECIMAT in Vigo and Norwegian citizen scientists from 'Lei en biolog' who collected some of the berried females in Vigo, Bergen, and Trondheim, respectively. Technical staff at IMR, NTNU, and NIBIO are thanked for providing approved holding tanks for collected crabs at Austevoll Research Station, Trondhjem Biological Station and NIBIO marine laboratory Bodø, Norway. We thank Fredrik Broms and Sabrina Hüpperling for their support in collecting crabs in Northern Norway. We are thankful to Eva and Helmes Geißel for lending us their caravan and facilitating the collection of crabs in Northern Norway. We are grateful to Julia Haafke (AWI) for performing the elemental analysis and to Fiona Bravo, Anne Fröhle, and Ella Tekotte for their help with larval rearing. This study has been conducted using E.U. Copernicus Marine Service Information; https://doi.org/10.48670/moi-00165. No permits were required for the field collection of crabs. Open Access funding enabled and organized by Projekt DEAL.

Disclosure

Human or animal rights: 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 22 September 2010) on the protection of animals used for scientific purposes. In addition, this research complies with the European regulation (No. 511/2014) regarding access to genetic resources and the fair and equitable sharing of benefits arising from their utilisation (Nagoya protocol). Authorisation to access Spanish genetic resources (*Carcinus maenas*): Ref. ESNC68, CSV: GEN-8e2b-06b0-12a7-b306-7d90-4683-1db3-ed89.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data for this paper will be available from DRYAD (https://doi.org/10.5061/dryad.hdr7sqvtw).

References

Alfred-Wegener-Institut Helmholtz-Zentrum für Polar-und Meeresforschung. 2023. "Marine Stations Helgoland and Sylt Operated by the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research." *Journal of Large-Scale Research Facilities* 8: 184. https://doi.org/10.17815/jlsrf-8-184.

Anger, K. 1996. "Physiological and Biochemical Changes During Lecithotrophic Larval Development and Early Juvenile Growth in the Northern Stone Crab, *Lithodes maja* (Decapoda: Anomura)." *Marine Biology* 126, no. 2: 283–296. https://doi.org/10.1007/BF00347453.

Anger, K. 1998. "Patterns of Growth and Chemical Composition in Decapod Crustacean Larvae." *Invertebrate Reproduction & Development* 33, no. 2–3: 159–176. https://doi.org/10.1080/07924259.1998.9652629.

Anger, K. 2001. *The Biology of Decapod Crustacean Larvae*. Vol. 14. A.A. Balkema.

Anger, K., and J. Harms. 1990. "Elemental (CHN) and Proximate Biochemical Composition and Decapod Crustacean Larvae." *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry* 97, no. 1: 69–80. https://doi.org/10.1016/0305-0491(90)90180-2.

Anger, K., E. Spivak, and T. Luppi. 1998. "Effects of Reduced Salinities on Development and Bioenergetics of Early Larval Shore Crab, *Carcinus maenas*." *Journal of Experimental Marine Biology and Ecology* 220, no. 2: 287–304. https://doi.org/10.1016/S0022-0981(97)00110-X.

Angilletta, M. J., Jr. 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis* (online edn). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198570875.001.1.

Bakke, S., S. I. Siikavuopio, and J. S. Christiansen. 2019. "Thermal Behaviour of Edible Crab *Cancer pagurus* Linnaeus, 1758 in Coastal Norway." *Fauna Norvegica* 39: 1–11. https://doi.org/10.5324/fn.v39i0.2738.

Baldanzi, S., D. Storch, S. A. Navarrete, M. Graeve, and M. Fernández. 2018. "Latitudinal Variation in Maternal Investment Traits of the Kelp Crab *Taliepus dentatus* Along the Coast of Chile." *Marine Biology* 165, no. 2: 37. https://doi.org/10.1007/s00227-018-3294-2.

Beaugrand, G., C. Luczak, and M. Edwards. 2009. "Rapid Biogeographical Plankton Shifts in the North Atlantic Ocean." *Global Change Biology* 15, no. 7: 1790–1803. https://doi.org/10.1111/j.1365-2486.2009.01848.x.

Beaugrand, G., P. C. Reid, F. Ibañez, J. A. Lindley, and M. Edwards. 2002. "Reorganization of North Atlantic Marine Copepod Biodiversity and Climate." *Science* 296, no. 5573: 1692–1694. https://doi.org/10.1126/science.1071329.

Behrens Yamada, S. 2001. *Global Invader: The European Green Crab*. Oregon Sea Grant; Washington Sea Grant.

Behrens Yamada, S., B. R. Dumbauld, A. Kalin, C. E. Hunt, R. Figlar-Barnes, and A. Randall. 2005. "Growth and Persistence of a Recent Invader *Carcinus maenas* in Estuaries of the Northeastern Pacific." *Biological Invasions* 7, no. 2: 309–321. https://doi.org/10.1007/s10530-004-0877-2.

Behrens Yamada, S., J. L. Fisher, and P. M. Kosro. 2021. "Relationship Between Ocean Ecosystem Indicators and Year Class Strength of the Invasive European Green Crab (*Carcinus maenas*)." *Progress in Oceanography* 196: 102618. https://doi.org/10.1016/j.pocean.2021.102618.

Behrens Yamada, S., R. E. Thomson, G. E. Gillespie, and T. C. Norgard. 2017. "Lifting Barriers to Range Expansion: The European Green Crab *Carcinus maenas* (Linnaeus, 1758) Enters the Salish Sea." *Journal of Shellfish Research* 36, no. 1: 201–208. https://doi.org/10.2983/035.036.0121.

Boersma, M., N. Grüner, N. Tasso Signorelli, P. E. Montoro González, M. A. Peck, and K. H. Wiltshire. 2016. "Projecting Effects of Climate Change on Marine Systems: Is the Mean all That Matters?" *Proceedings of the Royal Society B: Biological Sciences* 283, no. 1823: 20152274. https://doi.org/10.1098/rspb.2015.2274.

Brander, K., G. Blom, M. Borges, et al. 2003. "Changes in Fish Distribution in the Eastern North Atlantic: Are We Seeing a Coherent Response to Changing Temperature?" *ICES Marine Science Symposia* 219: 261–270.

Brattegard, T. 2011. *Endringer i Norsk Marin Bunnfauna 1997–2010 (No. Utredning for DN 2011–8)*. Direktoratet for Naturforvaltning; ISBN (PDF): 978–82–7072-928-9.

Byrne, M. 2006. "Life History Diversity and Evolution in the Asterinidae." *Integrative and Comparative Biology* 46, no. 3: 243–254. https://doi.org/10.1093/icb/icj033.

Chan, F. T., and E. Briski. 2017. "An Overview of Recent Research in Marine Biological Invasions." *Marine Biology* 164, no. 6: 121. https://doi.org/10.1007/s00227-017-3155-4.

Chust, G., E. Villarino, M. McLean, et al. 2024. "Cross-Basin and Cross-Taxa Patterns of Marine Community Tropicalization and Deborealization in Warming European Seas." *Nature Communications* 15, no. 1: 2126. https://doi.org/10.1038/s41467-024-46526-y.

Clarke, A. 1993. "Reproductive Trade-Offs in Caridean Shrimps." *Functional Ecology* 7, no. 4: 411. https://doi.org/10.2307/2390028.

Cohen, A. N., J. T. Carlton, and M. C. Fountain. 1995. "Introduction, Dispersal and Potential Impacts of the Green Crab *Carcinus maenas* in San Francisco Bay." *Marine Biology* 122: 225–237.

Compton, T. J., J. R. Leathwick, and G. J. Inglis. 2010. "Thermogeography Predicts the Potential Global Range of the Invasive European Green Crab (*Carcinus maenas*)." *Diversity and Distributions* 16, no. 2: 243–255. https://doi.org/10.1111/j.1472-4642.2010.00644.x.

Conover, D. O. 1992. "Seasonality and the Scheduling of Life History at Different Latitudes." *Journal of Fish Biology* 41: 161–178. https://doi.org/10.1111/j.1095-8649.1992.tb03876.x.

Cooper, B. S., B. H. Williams, and M. J. Angilletta. 2008. "Unifying Indices of Heat Tolerance in Ectotherms." *Journal of Thermal Biology* 33, no. 6: 320–323. https://doi.org/10.1016/j.jtherbio.2008.04.001.

Copernicus Climate Change Service/ECMWF. 2022. "Surface Air Temperature for June 2022." Data source: ERA5. https://climate.copernicus.eu/surface-air-temperature-june-2022.

Dawirs, R. R. 1980. "Elemental Composition (C,N,H) in Larval and Crab-I Stages of *Pagurus bernhardus* (Decapoda, Paguridae) and *Carcinus maenas* (Decapoda, Portunidae)." *Marine Biology* 57: 17–23.

Dawirs, R. R. 1982. "Methodical Aspects of Rearing Decapod Larvae, *Pagurus bernhardus* (Paguridae) and *Carcinus maenas* (Portunidae)." *Helgoländer Wissenschaftliche Meeresuntersuchungen* 35, no. 4: 439–464. https://doi.org/10.1007/BF01999134.

Dawirs, R. R. 1986. "Influence of Limited Food Supply on Growth and Elemental Composition (C, N, H) of *Carcinus maenas* (Decapoda) Larvae, Reared in the Laboratory." *Marine Ecology Progress Series* 31: 301–308. https://doi.org/10.3354/meps031301.

Dawirs, R. R. 1987. "Influence of Limited Starvation Periods on Growth and Elemental Composition (C,N,H) of *Carcinus maenas* (Decapoda: Portunidae) Larvae Reared in the Laboratory." *Marine Biology* 93, no. 4: 543–549. https://doi.org/10.1007/BF00392792.

Dawirs, R. R., C. Püschel, and F. Schorn. 1986. "Temperature and Growth in *Carcinus maenas* L. (Decapoda: Portunidae) Larvae Reared in the Laboratory From Hatching Through Metamorphosis." *Journal of Experimental Marine Biology and Ecology* 100, no. 1–3: 47–74. https://doi.org/10.1016/0022-0981(86)90155-3.

deRivera, C. E., N. G. Hitchcock, S. J. Teck, B. P. Steves, A. H. Hines, and G. M. Ruiz. 2007. "Larval Development Rate Predicts Range Expansion of an Introduced Crab." *Marine Biology* 150, no. 6: 1275–1288. https://doi.org/10.1007/s00227-006-0451-9.

Eckert, G. L. 2003. "Effects of the Planktonic Period on Marine Population Fluctuations." *Ecology* 84, no. 2: 372–383. https://doi.org/10.1890/0012-9658(2003)084[0372:EOTPPO]2.0.CO;2.

Emlet, R. B. 1995. "Developmental Mode and Species Geographic Range in Regular Sea Urchins (Echinodermata: Echinoidea)." *Evolution* 49, no. 3: 476–489. https://doi.org/10.1111/j.1558-5646.1995.tb02280.x.

Ens, N. J., B. Harvey, M. M. Davies, et al. 2022. "The Green Wave: Reviewing the Environmental Impacts of the Invasive European Green Crab (*Carcinus maenas*) and Potential Management Approaches." *Environmental Reviews* 30, no. 2: 59. https://doi.org/10.1139/er-2021-0059.

Fox, C. W., M. S. Thakar, and T. A. Mousseau. 1997. "Egg Size Plasticity in a Seed Beetle: An Adaptive Maternal Effect." *American Naturalist* 149, no. 1: 149–163. https://doi.org/10.1086/285983.

Gaitán-Espitia, J. D., L. D. Bacigalupe, T. Opitz, N. A. Lagos, S. Osores, and M. A. Lardies. 2017. "Exploring Physiological Plasticity and Local Thermal Adaptation in an Intertidal Crab Along a Latitudinal Cline." *Journal of Thermal Biology* 68: 14–20. https://doi.org/10.1016/j.jtherbio.2017.02.011.

Gaitán-Espitia, J. D., L. D. Bacigalupe, T. Opitz, N. A. Lagos, T. Timmermann, and M. A. Lardies. 2014. "Geographic Variation in Thermal Physiological Performance of the Intertidal Crab Petrolisthes Violaceus Along a Latitudinal Gradient." *Journal of Experimental Biology* 217: jeb.108217. https://doi.org/10.1242/jeb.108217.

García Molinos, J., B. S. Halpern, D. S. Schoeman, et al. 2016. "Climate Velocity and the Future Global Redistribution of Marine Biodiversity." *Nature Climate Change* 6, no. 1: 83–88. https://doi.org/10.1038/nclimate2769.

GBIF. 2023. "GBIF.org *Carcinus maenas* (21 November 2023)." GBIF. https://doi.org/10.15468/dl.aghsjj.

Geißel, J. P., N. Espinosa-Novo, L. Gimenéz, et al. n.d. "Larval Physiological Responses to Temperature Across the European Distribution Range of a Global Invader at Home: The Shore Crab *Carcinus maenas*." *Ecology and Evolution*. Online ahead of print.

Geißel, J. P., N. Espinosa-Novo, L. Giménez, et al. 2024. "Interactive Responses to Temperature and Salinity in Larvae of the Asian Brush-Clawed Crab Hemigrapsus Takanoi: Relevance for Range Expansion Into the Baltic Sea, in the Context of Climate Change." *Biological Invasions* 26: 1685–1704. https://doi.org/10.1007/s10530-024-03279-5.

George, S. B. 1995. "Echinoderm Egg and Larval Quality as a Function of Adult Nutritional State." *Oceanologica Acta* 19, no. 3–4: 297–308.

Gerland, S., R. B. Ingvaldsen, M. Reigstad, et al. 2023. "Still Arctic?-The Changing Barents Sea." *Elementa: Science of the Anthropocene* 11, no. 1: 00088. https://doi.org/10.1525/elementa.2022.00088.

Giménez, L. 2020. "Phenotypic Plasticity and Phenotypic Links in Larval Development." In *Developmental Biology and Larval Ecology: The Natural History of the Crustacea*, edited by M. Thiel, K. Anger, and S. Harzsch, vol. 7, 285–309. Oxford University Press.

Giménez, L., M. Boersma, and K. H. Wiltshire. 2024. "A Multiple Baseline Approach for Marine Heatwaves." *Limnology and Oceanography* 69, no. 3: 638–651. https://doi.org/10.1002/lno.12521.

Glazier, D. S. 1992. "Effects of Food, Genotype, and Maternal Size and Age on Offspring Investment in *Daphnia magna*." *Ecology* 73, no. 3: 910–926. https://doi.org/10.2307/1940168.

González-Ortegón, E., and L. Giménez. 2014. "Environmentally Mediated Phenotypic Links and Performance in Larvae of a Marine Invertebrate." *Marine Ecology Progress Series* 502: 185–195. https://doi.org/10.3354/meps10708.

Grosholz, E. D., and G. M. Ruiz. 1995. "Spread and Potential Impact of the Recently Introduced European Green Crab, *Carcinus maenas*, in Central California." *Marine Biology* 122, no. 2: 239–247. https://doi.org/10.1007/BF00348936.

Gurevitch, J., G. A. Fox, G. M. Wardle, Inderjit, and D. Taub. 2011. "Emergent Insights From the Synthesis of Conceptual Frameworks for Biological Invasions: Conceptual Frameworks for Biological Invasions." *Ecology Letters* 14, no. 4: 407–418. https://doi.org/10.1111/j.1461-0248.2011.01594.x.

Harms, J., B. Meyer-Harms, R. R. Dawirs, and K. Anger. 1994. "Growth and Physiology of *Carcinus maenas* (Decapoda, Portunidae) Larvae in the Field and in Laboratory Experiments." *Marine Ecology Progress Series* 108: 107–118. https://doi.org/10.3354/meps108107.

Haubrock, P. J., I. Soto, D. A. Ahmed, et al. 2024. "Biological Invasions Are a Population-Level Rather Than a Species-Level Phenomenon." *Global Change Biology* 30: e17312. https://doi.org/10.1111/gcb.17312.

Huang, B., Z. Wang, X. Yin, et al. 2021. "Prolonged Marine Heatwaves in the Arctic: 1982–2020." *Geophysical Research Letters* 48, no. 24: e2021GL095590. https://doi.org/10.1029/2021GL095590.

IPCC. 2023. *Climate Change 2022—Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change—Intergovernmental Panel on Climate Change*. 1st ed. Cambridge University Press. https://doi.org/10.1017/9781009325844.

Jacobs, Z. L., F. Jebri, S. Wakelin, et al. 2024. "Marine Heatwaves and Cold Spells in the Northeast Atlantic: What Should the UK Be Prepared for?" *Frontiers in Marine Science* 11: 1434365. https://doi.org/10.3389/fmars.2024.1434365.

Kelley, A. L., C. E. De Rivera, E. D. Grosholz, G. M. Ruiz, S. Behrens Yamada, and G. Gillespie. 2015. "Thermogeographic Variation in Body Size of *Carcinus maenas*, the European Green Crab." *Marine Biology* 162, no. 8: 1625–1635. https://doi.org/10.1007/s00227-015-2698-5.

Klassen, G., and A. Locke. 2007. *A Biological Synopsis of the European Green Crab,* Carcinus maenas. Government of Canada Publications.

Landeira, J. M., K. Matsuno, A. Yamaguchi, T. Hirawake, and T. Kikuchi. 2017. "Abundance, Development Stage, and Size of Decapod Larvae Through the Bering and Chukchi Seas During Summer." *Polar Biology* 40, no. 9: 1805–1819. https://doi.org/10.1007/s00300-017-2103-6.

Levin, L. A., and T. S. Bridges. 1995. "Chapter 1 Pattern and Diversity in Reproduction and Development." In *Ecology of Marine Invertebrate Larvae*, edited by L. McEdward, 1st ed., 1–48. CRC Press.

Levitan, D. R. 2000. "Optimal Egg Size in Marine Invertebrates: Theory and Phylogenetic Analysis of the Critical Relationship Between Egg Dize and Development Time in Echinoids." *American Naturalist* 156, no. 2: 175–192. https://doi.org/10.1086/303376.

Lien, V. S., R. P. Raj, and S. Chatterjee. 2024. "Surface and Bottom Marine Heatwave Characteristics in the Barents Sea: A Model Study." In *8th Edition of the Copernicus Ocean State Report (OSR8)*, edited by K. Von Schuckmann, L. Moreira, M. Grégoire, et al. Copernicus GmbH. https://doi.org/10.5194/sp-4-osr8.

Lindgren, B., and A. Laurila. 2010. "Are High-Latitude Individuals Superior Competitors? A Test With *Rana temporaria* Tadpoles." *Evolutionary Ecology* 24, no. 1: 115–131. https://doi.org/10.1007/s10682-009-9294-4.

Lindley, J. A. 1998. "Diversity, Biomass and Production of Decapod Crustacean Larvae in a Changing Environment." *Invertebrate Reproduction & Development* 33, no. 2–3: 209–219. https://doi.org/10.1080/07924259.1998.9652633.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. "100 of the World's Worst Invasive Alien Species: A Selection From the Global Invasive Species Database." In *Encyclopedia of Biological Invasions*, 1–12. Invasive Species Specialist Group (ISSG) a Specialist Group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN). https://doi.org/10.1525/9780520948433-159.

Mackenzie, B. R., and D. Schiedek. 2007. "Daily Ocean Monitoring Since the 1860s Shows Record Warming of Northern European Seas." *Global Change Biology* 13, no. 7: 1335–1347. https://doi.org/10.1111/j.1365-2486.2007.01360.x.

Madeira, D., L. Narciso, H. N. Cabral, and C. Vinagre. 2012. "Thermal Tolerance and Potential Impacts of Climate Change on Coastal and Estuarine Organisms." *Journal of Sea Research* 70: 32–41. https://doi.org/10.1016/j.seares.2012.03.002.

Magnússon, J. T., S. J. Hawkins, L. Gunnarsdóttir, J. Svavarsson, and K. Gunnarsson. 2024. "Range Extension of Invasive Cancer Irroratus and Native *Carcinus maenas* Polewards in the Ascophyllum -Dominated Intertidal Zone in North-West Iceland." *Journal of the Marine Biological Association of the United Kingdom* 104: e3. https://doi.org/10.1017/S0025315423000905.

Marco-Herrero, E., A. Rodríguez, and J. A. Cuesta. 2012. "Morphology of the Larval Stages of *Macropodia czernjawskii* (Brandt, 1880) (Decapoda, Brachyura, Inachidae) Reared in the Laboratory." *Zootaxa* 3338, no. 1. https://doi.org/10.11646/zootaxa.3338.1.2.

Marshall, D. J., and M. Alvarez-Noriega. 2020. "Projecting Marine Developmental Diversity and Connectivity in Future Oceans." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 375, no. 1814: 20190450. https://doi.org/10.1098/rstb.2019.0450.

Marshall, D. J., T. F. Bolton, and M. J. Keough. 2003. "Offspring Size Affects the Post-Metamorphic Performance of a Colonial Marine Invertebrate." *Ecology* 84, no. 12: 3131–3137. https://doi.org/10.1890/02-0311.

Marshall, D. J., and M. J. Keough. 2007. "The Evolutionary Ecology of Offspring Size in Marine Invertebrates." *Advances in Marine Biology* 53: 1–60. https://doi.org/10.1016/S0065-2881(07)53001-4.

Marshall, D. J., A. K. Pettersen, and H. Cameron. 2018. "A Global Synthesis of Offspring Size Variation, Its Eco-Evolutionary Causes and Consequences." *Functional Ecology* 32, no. 6: 1436–1446. https://doi.org/10.1111/1365-2435.13099.

Marshall, D. J., and P. D. Steinberg. 2014. "Larval Size and Age Affect Colonization in a Marine Invertebrate." *Journal of Experimental Biology* 217: jeb.111781. https://doi.org/10.1242/jeb.111781.

Merilä, J., A. Laurila, A. T. Laugen, K. Räsänen, and M. Pahkala. 2000. "Plasticity in Age and Size at Metamorphosis in *Rana Temporaria* - Comparison of High and Low Latitude Populations." *Ecography* 23, no. 4: 457–465. https://doi.org/10.1111/j.1600-0587.2000.tb00302.x.

Mieszkowska, N., R. Leaper, P. Moore, et al. 2005. "Marine Biodiversity and Climate Change: Assessing and Predicting the Influence of Climatic Change Using Intertidal Rocky Shore Biota." Marine Biological Association Occasional Publications No. 20.

Monteiro, J. N., J. Bueno-Pardo, M. Pinto, M. A. Pardal, F. Martinho, and F. Leitão. 2023a. "Implications of Warming on the Morphometric and Reproductive Traits of the Green Crab, *Carcinus maenas*." *Fishes* 8, no. 10: 485. https://doi.org/10.3390/fishes8100485.

Monteiro, M., S. L. P. de Castro, S. C. Marques, R. Freitas, and U. M. Azeiteiro. 2023b. "An Emergent Treat: Marine Heatwaves—Implications for Marine Decapod Crustacean Species—An Overview." *Environmental Research* 229: 116004. https://doi.org/10.1016/j.envres.2023.116004.

Naylor, E. 1962. "Seasonal Changes in a Population of *Carcinus maenas* (L.) in the Littoral Zone." *Journal of Animal Ecology* 31, no. 3: 601. https://doi.org/10.2307/2055.

O'Connor, M. I., J. F. Bruno, S. D. Gaines, et al. 2007. "Temperature Control of Larval Dispersal and the Implications for Marine Ecology, Evolution, and Conservation." *Proceedings of the National Academy of Sciences of the United States of America* 104, no. 4: 1266–1271. https://doi.org/10.1073/pnas.0603422104.

Oliphant, A., and S. Thatje. 2013. "Per Offspring Investment Implications for Crustacean Larval Development: Evolutionary Insights Into Endotrophy and Abbreviated Development." *Marine Ecology Progress Series* 493: 207–217. https://doi.org/10.3354/meps10496.

Pallarés, S., J. A. Carbonell, F. Picazo, D. T. Bilton, A. Millán, and P. Abellán. 2024. "Intraspecific Variation of Thermal Tolerance Along Elevational Gradients: The Case of a Widespread Diving Beetle (Coleoptera: Dytiscidae)." *Insect Science*. https://doi.org/10.1111/1744-7917.13466.

Pandori, L. L. M., and C. J. B. Sorte. 2019. "The Weakest Link: Sensitivity to Climate Extremes Across Life Stages of Marine Invertebrates." *Oikos* 128, no. 5: 621–629. https://doi.org/10.1111/oik.05886.

Pettersen, A. K., C. R. White, R. J. Bryson-Richardson, and D. J. Marshall. 2019. "Linking Life-History Theory and Metabolic Theory Explains the Offspring Size-Temperature Relationship." *Ecology Letters* 22, no. 3: 518–526. https://doi.org/10.1111/ele.13213.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2019. "Nlme: Linear and Nonlinear Mixed Effects Models." R-package version 3.1–140. R Core Team. http://CRAN.R-project.org/package=nlme.

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, et al. 2013. "Global Imprint of Climate Change on Marine Life." *Nature Climate Change* 3, no. 10: 919–925. https://doi.org/10.1038/nclimate1958.

Pottier, P., S. Burke, R. Y. Zhang, et al. 2022. "Developmental Plasticity in Thermal Tolerance: Ontogenetic Variation, Persistence, and Future Directions." *Ecology Letters* 25, no. 10: 2245–2268. https://doi.org/10.1111/ele.14083.

Quinn, B. K. 2018. "Dramatic Decline and Limited Recovery of a Green Crab (*Carcinus maenas*) Population in the Minas Basin, Canada After the Summer of 2013." *PeerJ* 6: e5566. https://doi.org/10.7717/peerj.5566.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Reese, T. C., A. M. H. Blakeslee, L. C. Crane, et al. 2024. "Shift From Income Breeding to Capital Breeding With Latitude in the Invasive Asian Shore Crab *Hemigrapsus sanguineus*." *Scientific Reports* 14, no. 1: 6654. https://doi.org/10.1038/s41598-024-57434-y.

Rezende, E. L., F. Bozinovic, A. Szilágyi, and M. Santos. 2020. "Predicting Temperature Mortality and Selection in Natural Drosophila Populations." *Science* 369, no. 6508: 1242–1245. https://doi.org/10.1126/science.aba9287.

Rezende, E. L., L. E. Castañeda, and M. Santos. 2014. "Tolerance Landscapes in Thermal Ecology." *Functional Ecology* 28, no. 4: 799–809. https://doi.org/10.1111/1365-2435.12268.

Robertson, D. R., and R. Collin. 2015. "Inter- and Intra-Specific Variation in Egg Size Among Reef Fishes Across the Isthmus of Panama." *Frontiers in Ecology and Evolution* 2, no. 84: 1–15. https://doi.org/10.3389/fevo.2014.00084.

Rollinson, N., and L. Rowe. 2016. "The Positive Correlation Between Maternal Size and Offspring Size: Fitting Pieces of a Life-History Puzzle." *Biological Reviews* 91, no. 4: 1134–1148. https://doi.org/10.1111/brv.12214.

Roman, J. 2006. "Diluting the Founder Effect: Cryptic Invasions Expand a Marine Invader's Range." *Proceedings of the Royal Society B: Biological Sciences* 273, no. 1600: 2453–2459. https://doi.org/10.1098/rspb.2006.3597.

Roman, J., and S. R. Palumbi. 2004. "A Global Invader at Home: Population Structure of the Green Crab, *Carcinus maenas*, in Europe: Population Structure of the European Green Crab." *Molecular Ecology* 13, no. 10: 2891–2898. https://doi.org/10.1111/j.1365-294X.2004.02255.x.

Rutterford, L. A., S. D. Simpson, B. Bogstad, J. A. Devine, and M. J. Genner. 2023. "Sea Temperature Is the Primary Driver of Recent and Predicted Fish Community Structure Across Northeast Atlantic Shelf Seas." *Global Change Biology* 29, no. 9: 2510–2521. https://doi.org/10.1111/gcb.16633.

Sakai, S., and Y. Harada. 2001. "Why Do Large Mothers Produce Large Offspring? Theory and a Test." *American Naturalist* 157, no. 3: 348–359.

Sanford, E., S. B. Holzman, R. A. Haney, D. M. Rand, and M. D. Bertness. 2006. "Larval Tolerance, Gene Flow, and the Northern Geographic Range Limit of Fiddler Crabs." *Ecology* 87, no. 11: 2882–2894. https://doi.org/10.1890/0012-9658.

Šargač, Z., L. Giménez, E. González-Ortegón, S. Harzsch, N. Tremblay, and G. Torres. 2022. "Quantifying the Portfolio of Larval Responses to Salinity and Temperature in a Coastal-Marine Invertebrate: A Cross Population Study Along the European Coast." *Marine Biology* 169: 81. https://doi.org/10.1007/s00227-022-04062-7.

Šargač, Z., L. Giménez, S. Harzsch, J. Krieger, K. Fjordside, and G. Torres. 2021. "Contrasting Offspring Responses to Variation in Salinity and Temperature Among Populations of a Coastal Crab: A Maladaptive Ecological Surprise?" *Marine Ecology Progress Series* 677: 51–65. https://doi.org/10.3354/meps13851.

Shanks, A. L. 2009. "Pelagic Larval Duration and Dispersal Distance Revisited." *Biological Bulletin* 216, no. 3: 373–385. https://doi.org/10.1086/BBLv216n3p373.

Shirley, S. M., T. C. Shirley, and S. D. Rice. 1987. "Latitudinal Variation in the Dungeness Crab, *Cancer magister*: Zoeal Morphology Explained by Incubation Temperature." *Marine Biology* 95, no. 3: 371–376. https://doi.org/10.1007/BF00409567.

Siwertsson, A., U. Lindström, M. Aune, et al. 2024. "Rapid Climate Change Increases Diversity and Homogenizes Composition of Coastal Fish at High Latitudes." *Global Change Biology* 30, no. 5: e17273. https://doi.org/10.1111/gcb.17273.

Smith, K. E., M. Aubin, M. T. Burrows, et al. 2024. "Global Impacts of Marine Heatwaves on Coastal Foundation Species." *Nature Communications* 15, no. 1: 5052. https://doi.org/10.1038/s41467-024-49307-9.

Śniegula, S., F. Johansson, and V. Nilsson-Örtman. 2012. "Differentiation in Developmental Rate Across Geographic Regions: A Photoperiod Driven Latitude Compensating Mechanism?" *Oikos* 121, no. 7: 1073–1082. https://doi.org/10.1111/j.1600-0706.2011.20015.x.

Somero, G. N. 2005. "Linking Biogeography to Physiology: Evolutionary and Acclimatory Adjustments of Thermal Limits." *Frontiers in Zoology* 2, no. 1: 1. https://doi.org/10.1186/1742-9994-2-1.

South, A. 2011. "Rworldmap: A New R Package for Mapping Global Data." *R Journal* 3, no. 1: 35–43. https://doi.org/10.32614/RJ-2011-006.

Souza, A. T., M. Ilarri, J. Campos, F. O. Ribas, J. C. Marques, and I. Martins. 2022. "Boom and Bust: Simulating the Effects of Climate

Change on the Population Dynamics of a Global Invader Near the Edge of Its Native Range." *Science of the Total Environment* 851: 158294. https://doi.org/10.1016/j.scitotenv.2022.158294.

Spitzner, F., L. Giménez, R. Meth, S. Harzsch, and G. Torres. 2019. "Unmasking Intraspecific Variation in Offspring Responses to Multiple Environmental Drivers." *Marine Biology* 166, no. 8: 112. https://doi.org/10.1007/s00227-019-3560-y.

Storch, D., P. Santelices, J. Barria, K. Cabeza, H.-O. Pörtner, and M. Fernández. 2009. "Thermal Tolerance of Crustacean Larvae (Zoea I) in Two Different Populations of the Kelp Crab Taliepus Dentatus (Milne-Edwards)." *Journal of Experimental Biology* 212, no. 9: 1371–1376. https://doi.org/10.1242/jeb.030205.

Sunday, J., J. M. Bennett, P. Calosi, et al. 2019. "Thermal Tolerance Patterns Across Latitude and Elevation." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 374, no. 1778: 20190036. https://doi.org/10.1098/rstb.2019.0036.

Tepolt, C. K., and G. N. Somero. 2014. "Master of all Trades: Thermal Acclimation and Adaptation of Cardiac Function in a Broadly Distributed Marine Invasive Species, the European Green Crab, *Carcinus maenas*." *Journal of Experimental Biology* 217, no. 7: 1129–1138. https://doi.org/10.1242/jeb.093849.

Thatje, S., G. A. Lovrich, G. Torres, W. Hagen, and K. Anger. 2004. "Changes in Biomass, Lipid, Fatty Acid and Elemental Composition During the Abbreviated Larval Development of the Subantarctic Shrimp Campylonotus Vagans." *Journal of Experimental Marine Biology and Ecology* 301, no. 2: 159–174. https://doi.org/10.1016/j.jembe.2003.09.019.

Thiel, M., and T. Dernedde. 1994. "Recruitment of Shore Crabs *Carcinus maenas* on Tidal Flats: Mussel Clumps as an Important Refuge for Juveniles." *Helgoländer Wissenschaftliche Meeresuntersuchungen* 48, no. 2–3: 321–332. https://doi.org/10.1007/BF02367044.

Torres, G., R. R. Melzer, F. Spitzner, Z. Šargač, S. Harzsch, and L. Giménez. 2021. "Methods to Study Organogenesis in Decapod Crustacean Larvae. I. Larval Rearing, Preparation, and Fixation." *Helgoland Marine Research* 75, no. 1: 3. https://doi.org/10.1186/s10152-021-00548-x.

Torres, G., D. N. Thomas, N. M. Whiteley, D. Wilcockson, and L. Giménez. 2020. "Maternal and Cohort Effects Modulate Offspring Responses to Multiple Stressors." *Proceedings of the Royal Society B: Biological Sciences* 287, no. 1929: 20200492. https://doi.org/10.1098/rspb.2020.0492.

Van Doorslaer, W., and R. Stoks. 2005a. "Growth Rate Plasticity to Temperature in Two Damselfly Species Differing in Latitude: Contributions of Behaviour and Physiology." *Oikos* 111, no. 3: 599–605. https://doi.org/10.1111/j.1600-0706.2005.14335.x.

Van Doorslaer, W., and R. Stoks. 2005b. "Thermal Reaction Norms in Two Coenagrion Damselfly Species: Contrasting Embryonic and Larval Life-History Traits." *Freshwater Biology* 50, no. 12: 1982–1990. https://doi.org/10.1111/j.1365-2427.2005.01443.x.

Wassmann, P. 2011. "Arctic Marine Ecosystems in an Era of Rapid Climate Change." *Progress in Oceanography* 90, no. 1–4: 1–17. https://doi.org/10.1016/j.pocean.2011.02.002.

Weersing, K., and R. Toonen. 2009. "Population Genetics, Larval Dispersal, and Connectivity in Marine Systems." *Marine Ecology Progress Series* 393: 1–12. https://doi.org/10.3354/meps08287.

Weiss, M., S. Thatje, and O. Heilmayer. 2010. "Temperature Effects on Zoeal Morphometric Traits and Intraspecific Variability in the Hairy Crab Cancer Setosus Across Latitude." *Helgoland Marine Research* 64, no. 2: 125–133. https://doi.org/10.1007/s10152-009-0173-8.

Wickham, H. 2011. "The Split-Apply-Combine Strategy for Data Analysis." *Journal of Statistical Software* 40, no. 1: 1–29. https://doi.org/10.18637/jss.v040.i01.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Williams, B. G. 1967. "Laboratory Rearing of the Larval Stages of *Carcinus maenas* (L.) [Crustacea: Decapoda]." *Journal of Natural History* 2, no. 1: 121–126. https://doi.org/10.1080/00222936800770681.

Yamahira, K., M. Kawajiri, K. Takeshi, and T. Irie. 2007. "Inter-Vs. Intrapopulation Variation in Thermal Reaction Norms for Growth Rate: Evolution of Latitudinal Compensation in Ectotherms With a Genetic Constraint." *Evolution* 61, no. 7: 1577–1589. https://doi.org/10.1111/j.1558-5646.2007.00130.x.

Yorio, P., N. Suárez, T. Kasinsky, M. Pollicelli, C. Ibarra, and A. Gatto. 2020. "The Introduced Green Crab (*Carcinus maenas*) as a Novel Food Resource for the Opportunistic Kelp Gull (*Larus dominicanus*) in Argentine Patagonia." *Aquatic Invasions* 15, no. 1: 140–159. https://doi.org/10.3391/ai.2020.15.1.10.

Zeng, C., and E. Naylor. 1997. "Rhythms of Larval Release in the Shore Crab *Carcinus maenas* (Decapoda: Brachyura)." *Journal of the Marine Biological Association of the United Kingdom* 77, no. 2: 451–461. https://doi.org/10.1017/S0025315400071794.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology With R*. Springer New York. https://doi.org/10.1007/978-0-387-87458-6.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.