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RESEARCH ARTICLE

Larval development rate predicts range expansion of an introduced crab

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Abstract Introduced populations can cause ecological and economic damage and are difficult to eradicate once they have established. It is therefore important to be able to predict both where species may become established and their capacity to spread within recipient regions. Here, we use a new method to assess potential for intraregional spread of a marine crab introduced to North America, *Carcinus maenas*. We determined survivorship and development rates throughout a range of temperatures in the laboratory for *C. maenas* larvae from non-native populations on the Atlantic and Pacific coasts of North America. The larvae exhibited narrower physiological tolerances than adults, and no lab-cultured larvae completed larval development below 10.0°C or above 22.5°C. Survivorship peaked at intermediate water temperatures of 12.5–20.0°C, and development time decreased with increasing temperatures within this range. Based upon these laboratory development rates, we used nearshore sea-surface temperature data from both coasts of North America to predict development times required for larvae at different months and sites. Taken together, survivorship and development data indicate that *C. maenas* has the capacity to continue its northward spread and establish populations at numerous additional sites in North America. Moreover, decadal temperature data at two Alaskan sites predicted little variability in development duration across years, suggesting that development duration predictions are robust to interannual water temperature differences.

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Introduction

Biological invasions are on the rise and are leading to the increasing homogeneity of biological communities worldwide (Cohen and Carlton 1998; Ruiz et al. 2000). Invasions occur when species establish self-sustaining populations beyond their historical range limits, usually as a result of human transport. Though some species introductions are innocuous, many others are known to cause significant ecological or economic damage (OTA 1993; Mack et al. 2000; Pimentel et al. 2005).

Once established, non-native populations can spread rapidly and over great distances from the initial point of introduction (Grosholz 1996; Andow 1999). Human-mediated transport can contribute to such intraregional spread, as can unaided dispersal (Wasson et al. 2001). Many marine species have life stages that remain in the water column for days to months, creating the potential for transport by ocean currents. Self-dispersal generally occurs in species with longer larval duration times.

One major goal of invasion ecology is to predict the establishment and spread of non-native populations. Predicting which species can invade and spread to particular regions would help inform monitoring efforts

and develop strategies to minimize consequences. For example, such predictive capability could identify when and where to monitor, thus increasing the efficiency of early detection and eradication efforts. Eradication efforts are more likely to be successful when populations first arrive and are still small (Hobbs and Humphries 1995; Crooks and Soulé 1999). Prediction, however, has proved difficult because knowledge of the ecology of most species is limited. In addition, the biology of a species in its native range may not be applicable to the probability of survival, development, and reproduction in new areas if it should arrive.

This study explores an approach for estimating the potential northward range expansion of an introduced marine species in North America, the European green crab *Carcinus maenas*. *Carcinus maenas* has invaded the coasts of several continents then spread within each region. In addition to its native range, which extends from northern Africa to northern Europe, *C. maenas* now inhabits South Africa, Australia, and both coasts of North America (Carlton and Cohen 2003). European populations were the probable source for most of these invasions. However, *C. maenas* in western North America appears to have been a secondary introduction from eastern North America (Bagley and Geller 1999).

Once established in a recipient region, intraregional expansion of *C. maenas* has been episodic with rapid jumps between periods of relative stasis (Grosholz 1996; Thresher et al. 2003). In the West Atlantic, *C. maenas* spread from the mid Atlantic states northeastward into Maine and Nova Scotia in the 1930–1950s (Audet et al. 2003). These northern populations declined in the late 1950s and early 1960s, most likely due to the colder water temperatures of this period (Welch 1968; Audet et al. 2003). In the 1990s, northern populations increased in abundance again and expanded into the Gulf of Saint Lawrence (Audet et al. 2003). On the west coast of North America, quick northward expansion of *C. maenas* from San Francisco Bay coincided with an El Niño event in 1998 (Behrens Yamada and Hunt 2000; Behrens Yamada et al. 2005). The rate of range expansion has since slowed or halted and many of the East Pacific populations have been declining in size (Behrens Yamada and Hunt 2000; Behrens Yamada et al. 2005). *Carcinus maenas* was found as far north as Barkley and Clayoquot Sounds in British Columbia, Canada by 2000 (J. Morrison in Carlton and Cohen 2003 and in Audet et al. 2003) and is now also reported as far north as Esperanza Inlet, British Columbia (G. Gillespie & T. Therriault, personal communication).

Although further range expansion of *C. maenas* is a significant concern because of its impacts on benthic communities (Cohen et al. 1995; Grosholz and Ruiz 1996; Grosholz et al. 2000; McDonald et al. 2001), the factors that control its distribution are not resolved. Predation by native crabs can limit the distribution of *C. maenas* (Hunt and Behrens Yamada 2003; deRivera et al. 2005; McDonald et al. 2006). Water temperature has also been positively correlated with abundance and northward spread of *C. maenas* (Beukema 1991; Audet et al. 2003). Adult *C. maenas* survive temperatures of 0–30°C and salinities of 4 to over 34 ppt (Broekhuysen 1936; Crothers 1967; Beukema 1991), but larvae have narrower tolerances. Larvae died when cultured at 6 and 25°C in laboratory experiments on European populations (Dawirs 1982, 1985; Dawirs and Dietrich 1986; Mohamedeen and Hartnoll 1989; Nagaraj 1993). These previous studies only examined a few temperatures each.

Our goal was to test whether areas beyond the present range of *C. maenas* in North America could support complete larval development given historical and potential future sea surface temperatures. Because the crabs may adapt to local conditions, we cultured larvae from invasive populations on both coasts of North America. Larval survivorship and development rates across temperatures were compared to water temperatures along coastal North America to identify potential range expansion of *C. maenas*.

Suitable development temperature is just one of the requirements for timely, complete larval development and for successful establishment of *C. maenas* in new areas. Salinity, oxygen, ultraviolet light, pollution, advection, and sinking all affect larval mortality (reviewed in Morgan 1995). Larval growth rates are also affected by a variety of factors. For example Harms et al. (1994) found that field-collected *C. maenas* larvae were nutrition limited; they were limited by lipids, which are needed for growth. Similarly, Dawirs et al (1986) found growth rates and efficiencies increased with temperature and larval stage given greater food availability and feeding rates. Together these studies highlight that the interactive role of food availability and temperature must be considered. Nonetheless, temperature-dependent development rate alone helps to delimit the areas that can support larval development and so indicates limits of range expansion. Other restrictive factors, such as salinity, will be evaluated in a subsequent paper.

Materials and methods

Collection and care of females and larvae

We collected gravid *C. maenas* on the east and west coasts of the United States with traps and by hand. We

used multiple females from two sources so the results would be robust and more broadly applicable. Crabs with gray to orange eggs were collected from Tomales Bay, CA, USA, in January to March 2002 then again in March to June 2003, and from Casco Bay, Maine, in June to August 2002. Crabs were packed with ice packs in moistened newspaper and sent overnight by air-freight to the Smithsonian Environmental Research Center, Edgewater, MD, USA. Upon arrival at the laboratory, crabs were housed in individual aquaria placed in constant-temperature chambers maintained at 12.5°C. Crabs were fed crab-food pellets or squid on alternate days and were checked daily for larval release.

All water used for the females and their larvae was obtained from the Rhode River (a subestuary of the Chesapeake Bay), adjusted to 30 ppt with sea salts then filtered to 0.01 μm. Antibiotics and an antifungal agent (100 mg l^{-1} each of Penicillin, Streptomycin, and Chloramphenicol) were added to the water. Temperature chambers were kept on a 12 h light and 12 h dark photoperiod cycle. Culture containers and other equipment were soaked in deionized water then filtered saltwater for 3 days prior to use.

Carcinus maenas larvae develop through four zoeal stages followed by one megalopal stage before metamorphosis to juvenile and adult instars. Larval development encompasses hatching to the end of the megalopal stage. Soon after hatching (<1 day), active first zoeae were collected from aquaria and placed individually into isolated culture compartments for rearing through development to first crab instar. We used 18-well polystyrene parts boxes holding 20 ml of water per well as culture compartments. Larvae in these boxes were placed into various experimental temperature treatments (see below) and cultured through the first juvenile crab instar.

We changed the water every other day and added fresh food. Larvae were given algae (rotating cultures of *Nannochloropsis*, *Isochrysis*, and *Tetraselmus*), rotifers (*Brachionis plicatilis*) and newly hatched *Artemia* nauplii, so that food was not a limiting factor. Larvae that reached the megalopal stage were given more food and twice the volume of water. We added a 4 × 3 cm piece of Nittex mesh to each megalopal well to provide structure to settle on. Larvae were monitored daily and exuvia were removed. Occasionally a zoeal molt was missed, which became apparent at the molt to megalopa.

Temperature treatments

Constant temperature treatments

We examined the effect of temperature on survivorship and development duration by culturing larvae at 2.5°C intervals from 7.5 to 25.0°C and at 30.0°C. Zoeae from each brood were distributed across all the treatment levels within each experiment: we used 18 or 36 larvae from each female in each of the parallel temperature treatments. Each box of 18 larvae was stepped up or down 1°C h^{-1} from the hatching temperature of 12.5°C to the experimental temperatures. We used larvae from seven females from California and seven from Maine, USA, to replicate maternal source of larvae in both populations. Table 1 shows the number of larvae cultured per female from each population. Larvae from two females from Maine were removed from the experiment before they completed the megalopal stage.

To determine lower temperature tolerance and development thresholds of larvae, we cultured 18 larvae from each of seven California females collected in 2003 at each of four temperatures: 4.0, 5.0, 6.0, and 7.0°C (Table 1). We also cultured larvae from these females at 15.0°C to verify that survivorship of these larvae was similar to our other larval survivorship results.

Variable temperature treatments

We conducted a second experiment to test if our constant temperature data predicted development time when temperatures vary. We moved larvae once from one constant temperature incubator to another one 2.5°C warmer or cooler than the first after 7, 14, or 21 days. Starting and ending temperatures included 10.0, 12.5, 15.0, and 17.5°C; we moved larvae up from the lower three temperatures and down from the higher three temperatures. Thus, we encompassed the range of temperatures that had supported high survivorship in our earlier constant temperature treatments. We conducted these variable temperature treatments in 2002 using 18 larvae from seven Maine crabs in each treatment. These treatments ran concurrently with and in the same incubators as constant temperature treatments on sibling larvae from Maine crabs.

Statistics and model evaluation and application

Survivorship and development rate: constant temperature treatments

We report data for the zoeal period, the time from hatching until the molt to the megalopal stage, and for the whole larval period, the time from hatching until the molt to the first crab instar. We examined survivorship and development duration data using univariate two-tailed analyses. Each variable approximated the

Table 1 Number of replicate larvae cultured from each female from each collection site for all treatments

Temperature	No. of larvae from each of *N* California crabs	No. of larvae from each of *N* Maine crabs	Total no. of larvae
Low temperature treatments			
4.0	18 from 7		126
5.0	18 from 7		126
6.0	18 from 7		126
7.0	18 from 7		126
15.0	18 from 7		126
Total	630 larvae from 7 crabs		630, from 7
Constant temperature treatments			
7.5	36 from 4, 18 from 3		198
10.0	36 from 4, 18 from 3	18 from 7	324
12.5	36 from 4, 18 from 3	18 from 7	324
15.0	36 from 4, 18 from 3	18 from 7	324
17.5	36 from 4, 18 from 3	18 from 7	324
20.0	36 from 4, 18 from 3	18 from 7	324
22.5	36 from 3	18 from 7	234
25.0	36 from 4, 18 from 3	18 from 7	324
30.0	36 from 4		144
Total	1,638 from 7 crabs	882 from 7 crabs	2,520, from 14
Variable temperature treatments[a]			
10.0–12.5		18 from 7 for each of 1, 2 and 3 weeks	378
12.5–10.0		18 from 7 for each of 1, 2 and 3 weeks	378
12.5–15.0		18 from 7 for each of 1, 2 and 3 weeks	378
15.0–12.5		18 from 7 for each of 1, 2 and 3 weeks	378
15.0–17.5		18 from 7 for each of 1, 2 and 3 weeks	378
17.5–15.0		18 from 7 for each of 1, 2 and 3 weeks	378
Total		2,268 larvae from 7 crabs	2,268, from 7
Grand total	2,268 from 14 crabs	3,150 from 7 crabs	5,418, from 21

[a] *Note*: the variable temperature experiment ran concurrently with the constant temperature treatments from Maine

normal distribution once it was transformed. We report the standard error to compare the group means of data used in these analyses and otherwise report the mean and standard deviation.

Survivorship was calculated as the proportion of larvae from each female at each temperature treatment that survived from the start of the experiment to megalopa or first crab. Because we report the proportion survivorship per female per temperature, the survivorship sample size represents the number of broods per temperature, not the total number of larvae used. We evaluated survivorship as a function of temperature from 7.5 to 30.0°C using a polynomial regression on arcsine square root transformed values. We also examined the number of days zoeae survived as a function of low temperature (4.0–7.0°C) with a one-factor ANOVA on log-transformed values. We compared the survivorship at 15.0°C of the siblings of these low-temperature larvae to larvae previously cultured at 15.0°C, using a *t* test, to determine whether the results at low temperatures were due to temperature and not the time of the experiment.

We examined the effect of temperature on development with an ANOVA on the natural-log transformed development durations versus temperature (nominal) for zoeae (for 10.0–25.0°C) and larvae (for 12.5–22.5°C). We also examined whether the source of the crabs affected zoeal development duration using a crossed, nested three-factor ANOVA, with source population (Maine, California) and temperature (for 12.5–17.5°C) as fixed factors and mother crab as a random factor nested in source population. Survivorship was too low for Maine-derived zoeae to use higher temperatures or larval development duration in this analysis. Subsequently, *t* tests were used to identify the temperatures that had significant differences in development durations across source population.

Model evaluation: variable temperatures

We used a development model outlined by Anger (1983) and later Dawirs (1985) to examine the relationship between larval development duration and temperature. This model divides overall development duration into fractions of development that have occurred during each day at each temperature then sums these fractions across all temperatures experienced during development. This model assumes that

(a) there is a log-linear relationship between development duration and temperature, at least for the temperatures that larvae might experience, and (b) at a given temperature development proceeds at a constant rate throughout each larval stage. Day–degree models present an alternative option, one that uses physiological time, the cumulative thermal requirement for development (e.g. Baskerville and Emin 1969; Andrewartha and Birch 1973; Sharpe and DeMichele 1977; Taylor 1981). We did not use day–degree models because our data did not support the assumption that, between development thresholds, every thermal increment will yield the same amount of development.

We applied our lab results to spatially explicit recorded thermal regimes using the Anger (1983) model. Before using this model to predict development duration given water temperatures in nature, we had to verify that the model's development duration predictions closely matched observed development duration under variable temperature regimes. Therefore, we compared the model predictions, which are based on constant-temperature durations, to the development data from our variable-temperature experiments.

We used an iterative method to calculate predicted development duration for each variable temperature scenario (which used larvae from Maine crabs) and for 2003 North American water temperatures. First, we used the constant temperature development data from larvae of Maine crabs to create logarithmic regression lines of temperature-dependent development for different larval stages. We then calculated the predicted fraction of development that occurred each day, which equals the inverse of the development duration for the temperature of that day. For example, if our logarithmic regression equation predicted larval development takes 55 days at 15°C, then a larva will have completed 1/55th of its development after 1 day at 15°C. We subtracted this fraction from the total remaining development then repeated. Thus, at the end of the second day, the remaining development = 1 − [(1/development duration for the temperature on day 1) − (1/development time for the temperature on day 2)]. We repeated this process until development was complete (remaining development equaled 0). The first day upon which the remaining development was negative or zero was the predicted number of days that development would take given the temperature scenario.

Predictions of larval development in nature

We examined the potential for *C. maenas* to complete larval development north of its present range using two methods. First, for sites within and beyond the *C. maenas* North American ranges, we determined the number of contiguous days in 2003 that the water temperature exceeded 12.5 and 15.0°C, temperatures that we used in our lab culturing experiments.

We obtained water temperature data from National Oceanic and Atmospheric Administration's (NOAA) website of observed United States water levels and meteorological and oceanographic information (http://www.co-ops.nos.noaa.gov/data_res.html) and from Fisheries and Oceans Canada (DFO) (http://www.meds-sdmm.dfo-mpo.gc.ca/meds/databases/Wave/WAVE_e.html and http://www.eole.qc.dfo.ca/thermo/english/) for 31 sites within and north of the *C. maenas* range on both coasts of North America (Fig. 1): (a) six sites within the east coast range, (b) two east coast sites north of the range, (c) eight west coast within-range sites, and (d) 15 sites north of its west coast range. We selected these sites because they had the most complete water temperature data for 2003 and were spread throughout regions within and north of the *C. maenas* range on both coasts of North America. Most files included hourly temperature readings, and some had readings every 10 min. We calculated daily averages from these readings. Some files were missing temperature data for entire days, and we assumed the missing temperatures were the average of the three previous and three subsequent days' averages. All the NOAA thermometers are deployed at Coast Guard piers and similar nearshore structures. The DFO thermometer locations, however, were more variable. For example, some of the west coast locations were on offshore buoys in 18–228 m of water (British Columbia buoys C46206, C46131, C46204, and C46185). All temperature readings were from within 1 m of the surface.

We used our logarithmic regression equations to predict *C. maenas* larval development at the same 31 sites given their average daily water temperatures. We used the iterative method described above to create development duration scenarios starting at the first day of each month for April to September 2003 at these sites.

Because water temperatures fluctuate interannually, we also examined one of the warmer Alaskan sites, Ketchikan, and one of the cooler sites, Juneau, across a 10-year cycle using the methods from above and temperature data from July 1994 to June 2004 available from NOAA. We selected these two sites because they had complete temperature records for 10 straight years.

Finally, we predicted development duration at the 17 northern sites given a 2°C warming of the water to determine if dispersed *C. maenas* larvae would be more likely

Fig. 1 Location of sites with water temperature data examined in study. *Open circles* indicate sites within the present *C. maenas* range, while *filled circles* indicate sites north of the range. The two sites with 10 year of data are marked with *asterisks*

to succeed in new areas if water temperatures rose. We chose 2°C because it is a midpoint of the predicted range of ocean warming over the next 100 years (IPCC 2001).

Results

Survivorship: constant temperature treatments

Temperature strongly affected survivorship of larvae cultured in the laboratory (Fig. 2; Table 2). For all larval stages, survivorship peaked at the intermediate temperatures and plummeted at the experimental temperature extremes (7.5, 25.0, and 30.0°C treatments). Overall, average larval survival peaked at 17.5°C with 25.4 ± 6.6% survivorship from hatching to the first crab instar. However, survival peaked at higher temperatures later in the developmental sequence. For example, first zoeal survival peaked at 15.0°C (73.7 ± 4.8%, mean ± SE, survivorship), whereas megalopal survival peaked at 20.0°C (60.3 ± 7.9%).

All of the larvae cultured in 2003 at low temperatures, 4.0–7.0°C, died before reaching the megalopal stage ($n = 126$ zoeae per temperature) and survived for fewer days as temperature decreased (ANOVA: $F_{3,500} = 36.29$, $P < 0.0001$). All larvae died before reaching the second zoeal stage when cultured below 7.0°C, and before the third zoeal stage at 7.0°C. Sibling zoeae cultured at 15.0°C did not have significantly lower survivorship to the second zoeal stage than zoeae cultured in our earlier experiments on California crabs (t test: $t = 0.80$, $df = 12$, $P = 0.4411$).

Development duration: constant temperature treatments

Zoeal development duration decreased as temperature increased from 10.0°C, showing a negative, decelerating functional relationship of temperature on development duration (Fig. 3a; ANOVA, 10.0–25.0°C: $N = 659$, $r^2 = 0.68$, $F_{6,652} = 233.78$, $P < 0.0001$, Tukey–Kramer post hoc tests show all combinations significantly differed except 20.0°C from 22.5 and 25.0°C, and 22.5 from 25.0°C). Similarly, larval development (cumulative development to the end of the megalopal stage) decreased as temperature increased (Fig. 3b; 10.0–22.5°C: $F_{5,267} = 184.35$, $P < 0.0001$, all combinations significantly differ except 10.0°C from 12.5 and 15.0°C, and 20.0°C from 22.5°C).

The longest in-lab larval development was 83 days (at 12.5°C), and the longest development for the subset that successfully grew beyond the first crab instar took 65 days.

Zoeal duration differed between the two source populations (ANOVA 12.5–17.5°C: $N = 479$, $r^2 = 0.78$, source population $F_{1,12} = 7.26$, $P = 0.0195$; temperature $F_{2,24} = 56.95$, $P < 0.0001$; mother [population], random $F_{12,24} = 3.31$, $P = 0.0061$; population × temperature $F_{2,437} = 19.06$, $P < 0.0001$; mother [population] × temperature $F_{24,437} = 7.41$, $P < 0.0001$; all levels significantly

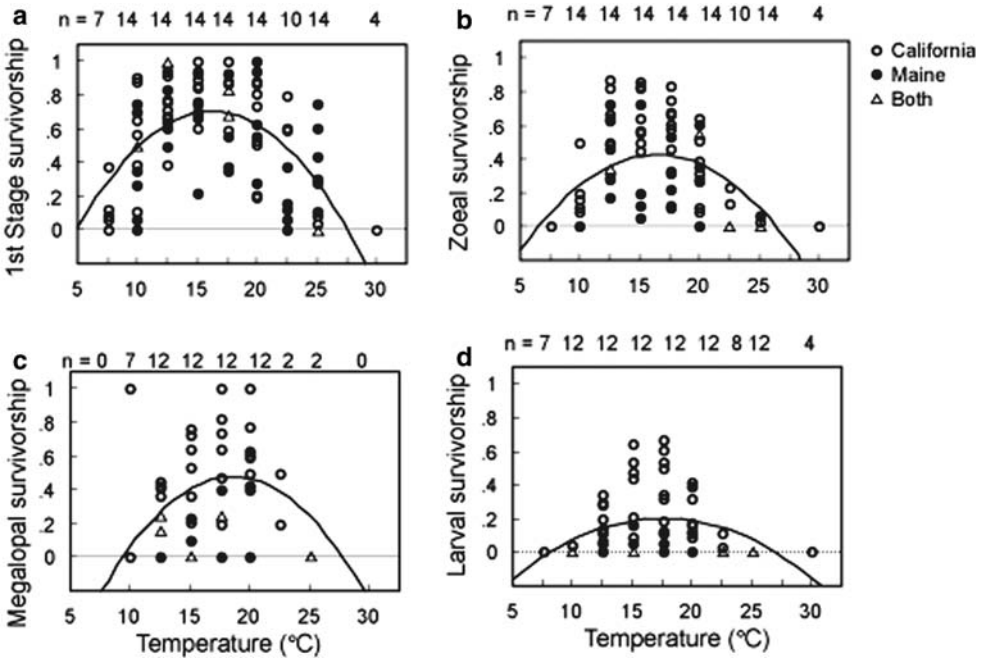

Fig. 2 Polynomial regression of proportion of larvae that survived per female versus temperature through **a** the first zoeal stage, **b** complete zoeal development, from hatching to the beginning of the megalopal stage, **c** the megalopal stage, and **d** complete larval development, from hatching to the beginning of the first crab instar. *Filled circles* indicate larval survival from Maine-derived brooding crabs, *open circles* indicate survival from California-derived crabs, and *open triangles* indicate larval survival from both populations**.** Equations are given in Table 2

Table 2 Polynomial regression statistics and equations of survivorship versus temperature for larvae from females captured in Maine ($n = 7$), in California ($n = 7$), and in both combined ($n = 14$; see also Fig. 2)

Stage	Maine larvae (N)	California larvae (N)	Both sources (N)
First zoeal	$r^2 = 0.31$, $F_{2,46} = 10.15$**	$r^2 = 0.61$., $F_{2,53} = 42.24$**	$r^2 = 0.47$., $F_{2,102} = 44.52$**
	$Y = -0.96 + 0.21X - 0.007X^2$	$Y = -0.82 + 0.19X - 0.006X^2$	$Y = -0.73 + 0.18X - 0.005X^2$
All four zoeal	$r^2 = 0.51$, $F_{2,46} = 24.30$**	$r^2 = 0.60$, $F_{2,53} = 40.28$**	$r^2 = 0.44$, $F_{2,102} = 39.56$**
	$Y = -1.33 + 0.20X - 0.006X^2$	$Y = -0.86 + 0.16X - 0.005X^2$	$Y = -0.74 + 0.14X - 0.004X^2$
Megalopal	$r^2 = 0.12$, $F_{2,18} = 1.17$	$r^2 = 0.40$, $F_{2,35} = 11.51$**	$r^2 = 0.18$, $F_{2,56} = 6.23$*
	$Y = -1.31 + 0.16X - 0.004X^2$	$Y = -2.20 + 0.32X - 0.009X^2$	$Y = -1.46 + 0.21X - 0.006X^2$
All larval	$r^2 = 0.26$, $F_{2,32} = 5.70$*	$r^2 = 0.33$, $F_{2,88} = 21.41$**	$r^2 = 0.33$, $F_{2,88} = 21.41$**
	$Y = -0.44 + 0.06X - 0.002X^2$	$Y = -0.65 + 0.11X - 0.003X^2$	$Y = -0.50 + 0.08X - 0.002X^2$

Regression statistics are based on transformed data (arcsine square root), whereas the polynomial equations for the regression lines are based on raw data

*$P < 0.01$, **$P < 0.0001$

differed). Students t tests used as post hocs showed zoeae from California developed significantly faster at 12.5 and 17.5°C than ones from Maine.

Development duration: variable temperature treatments

Figure 4 illustrates the regressions for zoeal and complete larval development of Maine-derived larvae, and Table 3 shows the logarithmic regression equations that describe development duration as a function of temperature for all stages and populations. The Maine larvae took longer duration than California larvae to develop at colder temperatures (Table 3) and so yielded more conservative predictions.

The predicted larval development durations derived from the Maine constant temperature data were similar to the observed durations for the larvae that were moved to a new temperature after 7, 14, or 21 days (Fig. 5). Larvae that were moved to a new temperature typically developed at a rate intermediate to larvae raised in a constant environment at the beginning and end temperatures (Fig. 5). Larval development duration decreased as the proportion of time spent at warmer temperatures increased (Fig. 5).

Predicted development in North America

Present conditions

Both our methods of examining potential larval development suggested that *C. maenas* could develop in several sites north of the present North American range limits. Given that average larval development in the

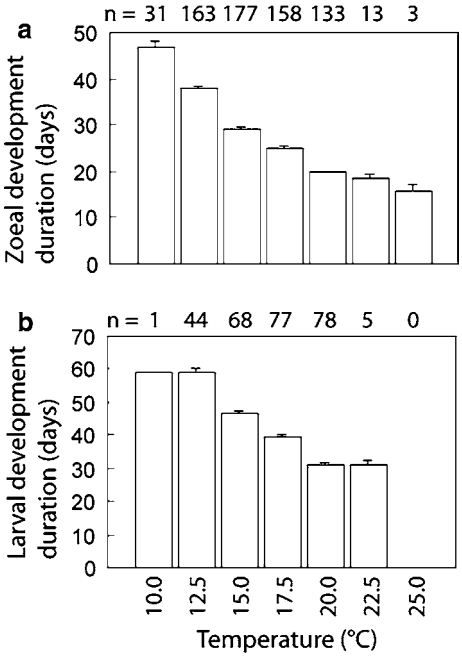

Fig. 3 Development duration (days) as a function of temperature (°C) for **a** zoeal development, and **b** larval development, for larvae from all crabs. Mean ± 1 SE; sample size, total number of larvae per temperature, given at *top*

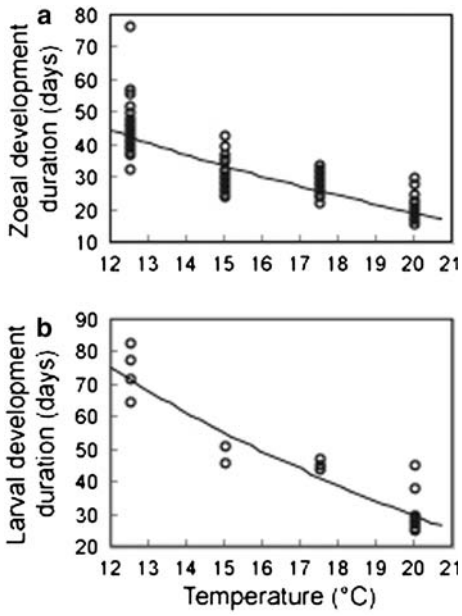

Fig. 4 Logarithmic regression of development time of **a** zoeal development (days) ($Y = 167.74 - 49.58$ ln temperature), and **b** larval development (days) ($Y = 296.55 - 89.19$ ln temperature) as a function of temperature (°C) for larvae of crabs from Maine

lab took 59 days at 12.5°C, 12 of 14 in-range sites (all but Humboldt and Yaquina) and 8 of 17 sites north of the range had enough days (>59 days) over 12.5°C for larvae to develop (Fig. 6a). Alternatively, using the minimum larval duration in culture (43 days) suggested Humboldt would also have enough warm days for complete development. None of the Alaskan sites would have enough warm days to support larval development if the cut-off were 83 days, the maximum larval duration at 12.5°C.

Many fewer of the in-range sites had enough days 15.0°C or above for complete larval development given the average development duration at 15.0°C (47 days), suggesting 12.5°C is a better measure (Fig. 6b). While all but three of the sites (Juneau, Unalaska, and Adak Is) had enough days over 10.0°C for larvae to complete development, laboratory larval survivorship was quite low (<1%) at 10.0°C.

Our second method, calculating development for fluctuating water temperatures, matched the predictions of our first method. The fastest predicted development times within the *C. maenas* range spanned 18–65 days on the east coast and 22–86 days (Yaquina Bay) on the west coast. Therefore, our data suggested the longest successful development duration would take between 65 days—the fastest development for a cold in-range site with a self-sustaining population (Bar Harbor)—and 72 days—the development predicted for an in-range site with low and decreasing abundance of *C. maenas* (Humboldt Bay). The sites that had enough days over 12.5°C to support development also had predicted development faster than 72 days (Figs. 7, 8). The fastest development north of the *C. maenas* range took from only 43–117 days,

Table 3 Logarithmic regression equations predicting the development duration (days) of different larval stages as a function of water temperature (°C)

Stage	Equation, Maine larvae (N)	Equation, California larvae (N)	Equation, both sources (N)
First zoeal	$39.83 - 11.70 \times \ln X$ (150)	$44.40 - 13.04 \times \ln X$ (234)	$42.34 - 12.43 \times \ln X$ (384)
Second zoeal	$33.45 - 9.65 \times \ln X$ (136)	$23.64 - 6.31 \times \ln X$ (180)	$27.48 - 7.60 \times \ln X$ (316)
Third zoeal	$40.01 - 11.78 \times \ln X$ (125)	$20.65 - 5.34 \times \ln X$ (294)	$25.02 - 6.74 \times \ln X$ (419)
Fourth zoeal	$63.51 - 19.54 \times \ln X$ (140)	$25.51 - 6.69 \times \ln X$ (401)	$32.24 - 8.91 \times \ln X$ (541)
All four zoeal	$167.74 - 49.58 \times \ln X$ (166)	$122.96 - 34.47 \times \ln X$ (493)	$130.46 - 36.93 \times \ln X$ (659)
Megalopal	$126.43 - 38.38 \times \ln X$ (29)	$77.76 - 21.72 \times \ln X$ (245)	$82.26 - 23.29 \times \ln X$ (274)
All larval	$296.29 - 89.09 \times \ln X$ (29)	$189.16 - 52.43 \times \ln X$ (245)	$199.03 - 55.87 \times \ln X$ (274)

Data were from the constant temperature treatments of larvae that lived until or beyond the megalopal stage for Maine-derived larvae, California-derived larvae, and for both population sources combined

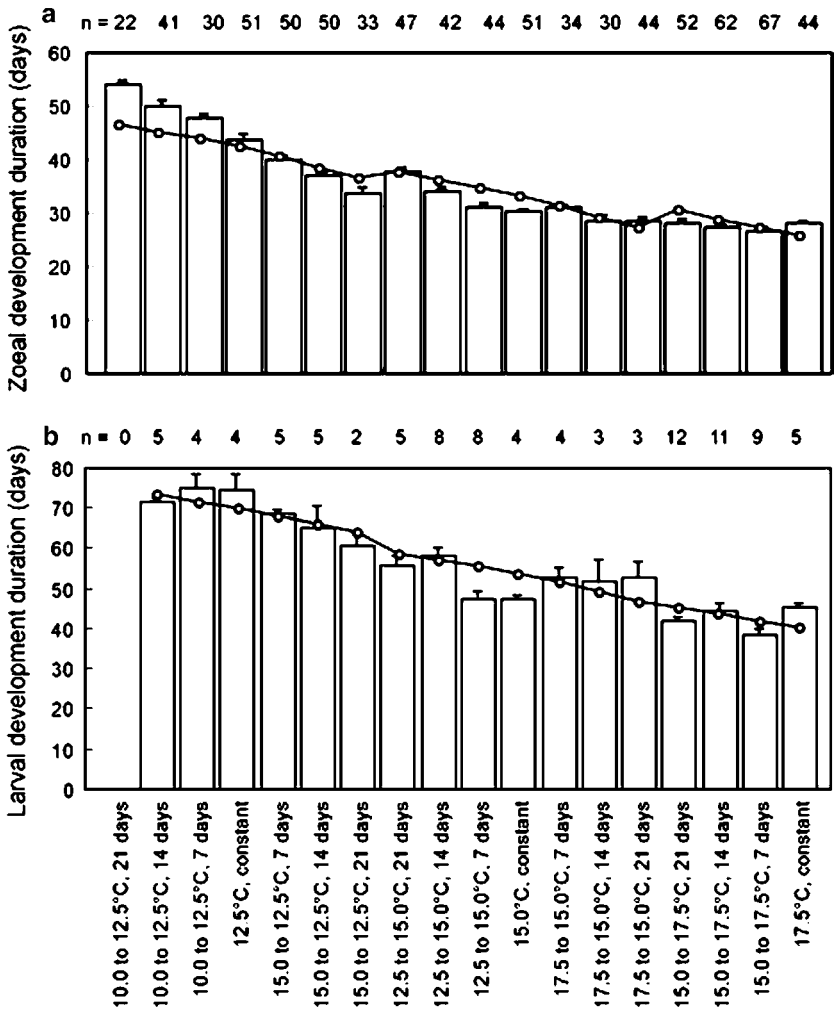

Fig. 5 Predicted development duration derived from the logarithmic regression line (*line with circles*) and observed (*bars*) development duration (days) for larvae at a constant temperature or moved after 7, 14, or 21 days to a new temperature (°C) for **a** zoeae, and **b** larvae from Maine crabs. *Bars* show means ± 1 SE; sample size given at *top*

indicating complete larval development is possible at some northern sites. Development within 83 days, the maximum successful larval development in lab, could occur at all but four sites (Fig. 8).

In addition to showing that many sites presently north of the *C. maenas* range could support complete larval development, our second method revealed other important patterns. First, the west coast north-of-range sites had the greatest changes in duration as the seasons progressed (Fig. 7) and so should be most affected by interannual variation. Second, larval development was fastest in August at sites within the present North American range of *C. maenas* and in July at sites north of the ranges (Fig. 7). Third, predicted development duration increased northward with the exception of Humboldt and Yaquina, which had long durations for their latitudes.

Our lab survivorship data suggested most to all larvae would die if exposed to more than 14 days below 6°C or more than 23 days below 7°C. In April 2003, prolonged cold water temperatures would likely cause mortality at four of the West Atlantic in-range sites, both of the northern ones, and nine of the East Pacific north-of-range sites. In May, the three eastern Canada sites and three of the Alaska sites (from Sand Point to Adak Is, AK, USA) also had a lethal number of cold days. Larvae hatched on 1 August or later would also have encountered too many cold days around Baie-Comeau, and seven Alaskan sites would be too cold for larvae hatched in September.

Variation across years and uniform warming

Predicted larval development duration fluctuated only moderately across years (Table 4). Early spring months showed greater interannual variability in development duration and temperature than early to mid summer, but never greater than a 15 day and 2.0°C difference between the most extreme years in waters off Ketchikan and Juneau, Alaska (Table 4).

Mimicking uniform warming by adding 2°C to the 2003 water temperatures revealed that all in-range sites

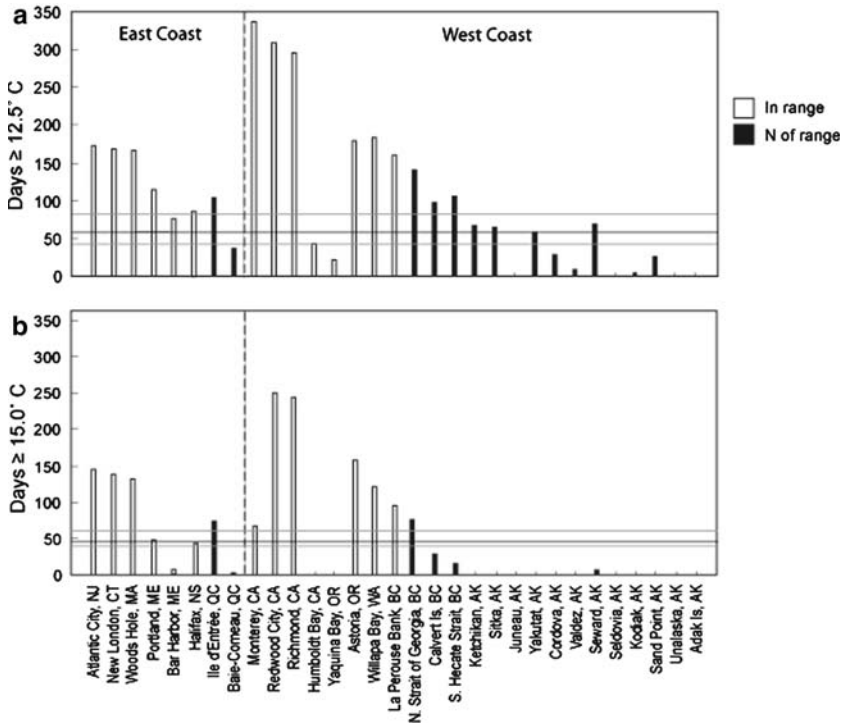

Fig. 6 Number of days in 2003 with water temperature above **a** 12.5°C and **b** 15.0°C at 6 eastern and 8 western North American sites within *C. maenas*'s present range and 2 eastern and 15 western sites north of the range. The *black line* shows average larval development duration (days) for our lab-cultured larvae at 12.5 and 15.0°C (59 and 47 days), while the *grey lines* denote the minimum and maximum development durations in laboratory for each temperature (43–83 and 40–60 days). Sites are arranged from south to north on the east and west coasts

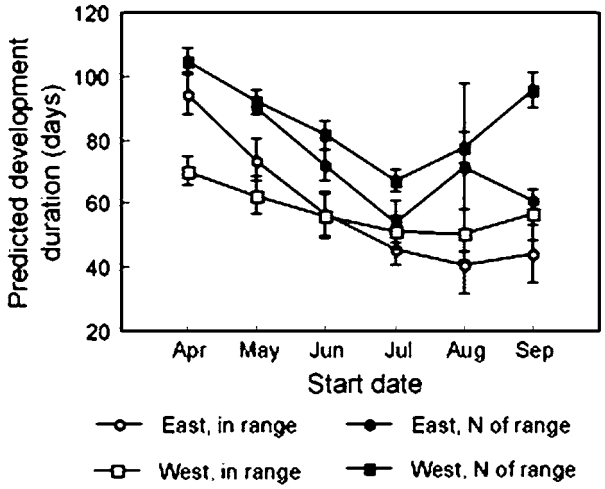

Fig. 7 Predicted larval development duration (days) using logarithmic regression equations and temperatures at NOAA and DFO sites in four regions, within the *C. maenas* ranges on the east and west coasts of North America and north-of-range on both coasts, starting on the first of each month from April through September 2003. Means ± 1 SE

plus 12 of 17 north-of-range sites would have 59 days above 12.5°C, an increase of four northern sites (all but Baie-Comeau, Juneau, Seldovia, Unalaska, and Adak Island, AK, USA). Larval development in the 17 areas north of the present *C. maenas* range would be completed after as few as 31 days total, 15.9 ± 5.3 days (mean ± SD) fewer (from 8 to 36 days fewer) than in 2003 (Fig. 8). Therefore, 14 of 17 of the north-of-range sites examined (all but Juneau, Unalaska, and Adak Island) would be within the range of predicted development duration of less than 72 days. In addition, the water temperature would only be lethal in April and only at the six most extreme sites, Halifax, Île d'Entrée, Baie-Comeau, Sand Point, Unalaska, and Adak Island.

Discussion and conclusions

Our data serve as a first step in identifying key areas for *C. maenas* monitoring north of its present ranges. The survivorship and development rate data from larvae cultured at nine temperatures suggest that *C. maenas* has the capacity to establish populations in multiple locations north of its present North American ranges, given other restrictive criteria are met. Two different methods identified 8 of 17 northern sites that met temperature requirements for *C. maenas* larval development. Not only did these eight sites experience enough days over 12.5°C to allow complete larval development, the required development time at each site was within the range of successful development in the lab and faster than that predicted for some sites that already have self-sustaining, abundant *C. maenas* populations. For example, the fastest predicted development for Bar Harbor area waters, which have many *C. maenas*, took at least 65 days, while eight sites north of the east and west coast ranges could support complete development in fewer days during summer

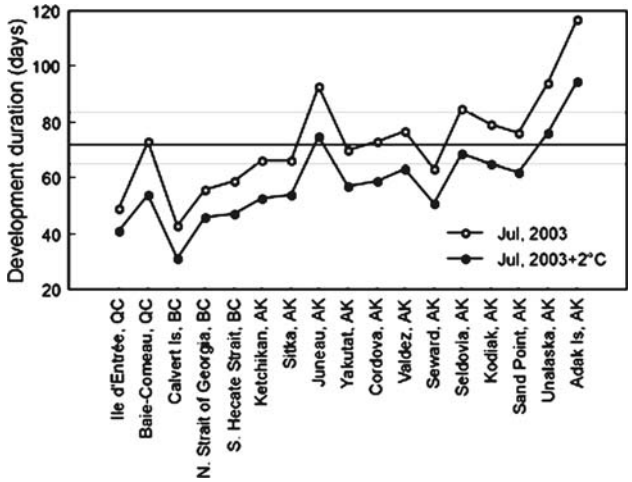

Fig. 8 Estimated larval development duration (days) using the logarithmic regression equations from our model and 2003 temperatures (*open circles*) and for 2°C added to 2003 temperatures (*filled circles*) at 17 sites north of *C. maenas*'s West Atlantic and East Pacific ranges, starting 1 July 2003. *Lines* are at 83 days (the longest successful development in lab), 65 days (the longest larval development duration of cultured larva that survived beyond the first crab instar), and 72 days (the fastest development for an in-range site with a low population of *C. maenas*)

months. If *C. maenas* arrive in these or other sites north of their present range limits, retention in warmer, shallow water areas could speed larval development and so reduce risks of larval death and increase the likelihood of establishing local populations.

Population establishment beyond the present ranges depends on a number of factors in addition to successful, timely larval development. First, the larvae must be able to develop completely before the water cools enough to stop development and must survive while in cold water. Survivorship of cultured larvae at temperatures below 12.5°C was very low due to extended exposure to cold. In addition, the long development time of larvae in water 12.5°C or colder would expose these larvae to several other threats. Prolonged development increases the likelihood of mortality due to exposure to other extreme environmental conditions (e.g. UV light) or cumulative predation risk.

Second, propagules would have to be transported to the area via ships or ocean currents, and larvae must remain in the area to develop. Alongshore flow recently emerged as an important contributing factor to range limits and population placement, and this would especially be important in cold waters. Larvae could be swept away from suitable nearshore megalopal settling sites as they slowly develop in cold waters (Queiroga et al. 1994). Moreover, Gaylord and Gaines (2000) showed current flow alone can limit distributions of marine species along the west coast of North America. Furthermore, they suggested that flow interacts with life history: organisms with brief larval stages can persist in higher flow than species with longer larval durations, which are more susceptible to flow-induced boundaries. Our results suggest that flow also can cause variable effects within a single species due to temperature-dependent development duration. More polar populations should be more vulnerable to extirpation by current flow because of the increased larval durations that result from cold water.

Third, arriving propagules would need suitable habitat upon which to settle. The topography of both coasts may also restrict the distribution of *C. maenas* in North America. Rocky substrate used by recruiting *C. maenas* megalopae is limited in the southern part of its West Atlantic range. Because it does not occupy exposed shores in the Northeast Pacific (Grosholz and Ruiz 1996), the long stretches between bays and inlets also may limit expansion south of Morro Bay, CA, USA. Salinity is also a restrictive factor for *C. maenas* larval survival (Nagaraj 1993; Anger et al. 1998).

Fourth, individuals would have to avoid predation and reproduce. Predation by the blue crab, *Callinectes sapidus*, decreases the abundance and distribution of *C. maenas* where these crabs overlap in the West Atlantic, Maryland to Massachusetts, and perhaps sets the southern range limit (deRivera et al. 2005). Similarly, predation by fish and native crabs affects *C. maenas* abundance, local distribution, and habitat use in the East Pacific (Hunt and Behrens Yamada 2003;

Table 4 Interannual variation (1994–2004) in predicted development duration (days) and mean monthly temperature (°C) across spring to late summer based on sea surface temperatures off Ketchikan and Juneau, Alaska

Variable	Ketchikan	Juneau
Maximum variation in development duration		
1 April	15 days [86 (1998)–101 days (2002)]	12 days [110 (2003)–122 days (2002)]
1 July	10 days [59 (2004)–69 days (2002)]	8 days [92 (1998)–100 days (2000)]
1 September	9 days [85 (1997,1999)–94 days (1996)]	23 days [120 (2002)–153 days (1996)]
Maximum variation in temperature		
April	2.0°C [6.2 (2002)–8.2°C (1998)]	1.8°C [3.9 (1996)–5.7°C (1998)]
July	1.8°C [12.7 (1996)–14.5°C (2004)]	1.3 [9.1 (2002)–10.4°C (2003)]
September	2.1°C [11.8 (2001)–13.9°C (2004)]	0.8°C [8.5 (1996)–9.3°C (1997)]

McDonald et al. 2003, 2006) and may provide biotic resistance to *C. maenas* across latitudes.

Our data provide minimum and maximum temperatures and durations for successful larval development and survival. Now, other restrictive factors, such as salinity and biotic resistance, should be examined for the coastal waters, especially bays, that occur within this identified range of limiting temperatures.

Based on our estimates, two sites within the present northeastern Pacific range of *C. maenas*, Humboldt and Yaquina Bays, were too cold in 2003 to allow for complete larval development. Moreover, predicted development time for Yaquina was longer than the longest development of cultured larvae. These predicted development times are not inconsistent with observations of these populations, however. Since the 1998 *C. maenas* invasion into Humboldt and Yaquina Bays, their abundance has decreased, and populations may not be self-sustained (E. D. Grosholz et al., unpublished data; Behrens Yamada et al. 2005), perhaps because of their low water temperatures.

Larvae from two North American populations we sampled averaged different development times. Larvae from California crabs developed faster than Maine-derived ones. This difference could be an artifact of lab methods such as the temporal difference in field collection of gravid females. Broods from different females also developed at significantly different rates, but the difference between populations exceeded maternal-based differences. Alternatively, the development rates of the two populations may differ due to plasticity or adaptation. Our lab temperature-dependent development durations were much shorter than those reported for three studies on European-collected crabs (Dawirs 1985; Dawirs and Dietrich 1986; Mohamedeen and Hartnoll 1989) but longer than those reported in a fourth European study (Nagaraj 1993). Clearly, more research is needed to examine differences between populations.

We used the more conservative of the two measures for our predictions, the development duration of larvae from Maine crabs. Therefore, if the development rate differences between the coasts reflect true variation between populations, introduced *C. maenas* may be able to complete development in more Northeast Pacific sites given the faster development of the nearby California populations.

Our analyses also provide a conservative estimate of temperature constraint to larval development because they estimate temperature limitation based upon measurements at a single location and depth for each site. Some shallow water reaches of bays and estuaries would be warmer than these measurement locations due to radiant heating over shallow flats. For example, on 5 July 2003, water temperature averaged 10.23°C at the NOAA thermometer off Seldovia, near the entrance of Kachemak Bay, while water temperature from three nearshore sites further into the bay averaged 18.9°C (FA Foster, personal communication). The extent to which warmer subhabitats affect larval development and distribution is not known for North America. Such fine-scale spatial variation may allow some reproduction in parts of Yaquina and Humboldt Bays and could increase the probability of successful establishment of self-sustaining populations north of the present range limits.

We found little variation in the predicted development durations across years from July 1994 through June 2004 in Ketchikan and Juneau, Alaska. This low variation suggested the 2003 data used for all other site assessments were representative and useful for predictions. However, Anger (1983) noted that the post-larval settlement period varied across years, with spring warming in cold years more strongly influencing development time than in warm years. Therefore, cold years had restricted settlement times (Anger 1983).

The low interannual variation also showed that uniform warming may have a greater effect on range expansion and range limits than most interannual variation. Increasing water temperatures by 2°C brought most of the examined northwestern sites within the predicted development duration range of existing North American *C. maenas* populations. Warming would also facilitate spread by decreasing the frequency of mortality from exposure and the likelihood of larval dilution or predation. Global or cyclical warming would speed development and so would decrease the probability of flow-mediated range limits for a species or would push the limits further poleward. Furthermore, Anger's (1983) finding of increased effects after cold years likely also applies to cold areas. Hence, northern waters affected by global climate change may be most strongly affected by warming sea temperatures.

The fastest predicted development during the past decade was for 1998, an El Niño year when *C. maenas* spread north from California to Washington (Behrens Yamada and Hunt 2000; Behrens Yamada et al. 2005). El Niños may facilitate spread in the East Pacific because the change in current direction can facilitate northward dispersal and because warmer water speeds larval development and increases survivorship. Even slight range expansion during warm or El Niño years is a threat because every step northward provides a closer source population for further spread and increases the probability of adaptation to the cooler water of the following years.

In conclusion, our results indicated that *C. maenas* larvae could complete development at multiple sites north of their range limits, suggesting risk of continued invasion under present conditions. The risk of invasion could increase even more due to expected future changes, including warmer water and an increase in human-mediated transport mechanisms as Alaska expands its development and commerce. As *C. maenas* spreads further north, each population has the potential for local adaptation and interactions with the environment, both of which could further increase spread.

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References

Andow DA (1999) Spread of invading organisms. In: Yano E, Matsuo K, Shiyomi M, Andow DA (eds) Biological invasions of ecosystem by pests and beneficial organisms. NIAES Series, vol 3. National Institute of Agro-Environmental Sciences, Tsukuba, Japan, pp 66–77

Andrewartha HG, Birch LC (1973) The history of insect ecology. In: Smith RF, Mittler TE, Smith CN (eds) History of entomology. Annual Reviews Inc, Palo Alto, pp 229–266

Anger K (1983) Temperature and the larval development of *Hyas araneus* L. (Decapoda: Majidae); extrapolation of laboratory data to field conditions. J Exp Mar Biol Ecol 69:203–215

Anger K, Spivak E, Luppi T (1998) Effects of reduced salinities on development and bioenergetics of early larval shore crab, *Carcinus maenas*. J Exp Mar Biol Ecol 220:287–304

Audet D, Davis DS, Miron G, Moriyasu M, Benhalima K, Campbell R (2003) Geographical expansion of a nonindigenous crab, *Carcinus maenas* (L.), along the Nova Scotian shore into the southeastern Gulf of St. Lawrence, Canada. J Shellfish Res 22:255–262

Bagley MJ, Geller JB (1999) Microsatellite DNA analysis of native and invading populations of European green crabs. In: Pederson J (ed) Marine bioinvasions: proceedings of the 1st national conference. MIT Press, New York, pp 37–39

Baskerville GL, Emin PE (1969) Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50:514–517

Behrens Yamada S, Hunt CE (2000) The arrival and spread of the European green crab, *Carcinus maenas*, in the Pacific Northwest. Driessena 11:1–7

Behrens Yamada S, Dumbauld BR, Kalin A, Hunt CE, Figlar-Barnes R, Randall A (2005) Growth and persistence of a recent invader *Carcinus maenas* in estuaries of the Northeastern Pacific. Biol Invasions 7:309–321

Beukema JJ (1991) The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. J Exp Mar Biol Ecol 153:97–113

Broekhuysen GJ Jr (1936) On development, growth and distribution of *Carcinides maenas* (L.). Arch Néerl Zool 2:257–399

Carlton JT, Cohen AN (2003) Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *C. aestuarii*. J Biogeogr 30:1809–1820

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279:555–558

Cohen AN, Carlton JT, Fountain MC (1995) Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Mar Biol 122:225–237

Crooks JA, Soulé ME (1999) Lag times in population explosions of invasive species: causes and implications. In: Sandlund OT, Schei PJ, Viken A (eds) Invasive species and biodiversity management. Kluwer, Dordrecht, pp 103–125

Crothers J (1967) The biology of the shore crab *Carcinus maenas* (L.). I. The background—anatomy, growth and life history. Field Stud 2:407–434

Dawirs RR (1982) Methodical aspects of rearing decapod larvae, *Pagurus bernhardus* (Paguridae) and *Carcinus maenas* L. (Portunidae). Helgol Meeresun 35:439–464

Dawirs RR (1985) Temperature and larval development of *Carcinus maenas* (Decapoda) in the laboratory; predictions of larval dynamics in the sea. Mar Ecol Prog Ser 24:297–302

Dawirs RR, Dietrich A (1986) Temperature and laboratory feeding rates in *Carcinus maenas* (Decapoda: Portunidae) larvae from hatching through metamorphosis. J Exp Mar Biol Ecol 99:133–148

Dawirs RR, Püschel C, Schorn F (1986) Temperature and growth in *Carcinus maenas* L. (Decapoda, Portunidae) larvae reared in the laboratory from hatching through metamorphosis. J Exp Mar Biol Ecol 100:47–74

deRivera CE, Ruiz GM, Hines AH, Jivoff P (2005) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. Ecology 86:3364–3376

Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. Am Nat 155:769–789

Grosholz ED (1996) Contrasting rates of spread for introduced species in terrestrial and marine systems. Ecology 77:1680–1686

Grosholz ED, Ruiz GM (1996) Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab, *Carcinus maenas*. Biol Conserv 78:59–66

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG (2000) The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206–1224

Harms J, Meyer-Harms B, Dawirs RR, Anger K (1994) Growth and physiology of *Carcinus maenas* (Decapoda, Portunidae) larvae in the field and in laboratory experiments. Mar Ecol Prog Ser 108:107–118

Hobbs RJ, Humphries SE (1995) An integrated approach to the ecology and management of plant invasions. Conserv Biol 9:761–770

Hunt CE, Behrens Yamada S (2003) Biotic resistance experienced by an invasive crustacean in a temperate estuary. Biol Invasions 5:33–43

IPCC, Intergovernmental Panel on Climate Change (2001) Climate change 2001: the scientific basis. In: Houghton JT et al (eds) Contribution of working group 1 to the third

assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710
McDonald PS, Jensen GC, Armstrong DA (2001) The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. J Exp Mar Biol Ecol 258:39–54
McDonald PS, Jensen GC, Armstrong DA (2003) Biotic resistance to European green crab, *Carcinus maenas*, by native analogs in the northeastern pacific. J Shellfish Res 22:606
McDonald PS, Holsman KK, Beauchamp DA, Dumbauld BR, Armstrong DA (2006) Bioenergetics modeling to investigate habitat use by the non-indigenous crab, *Carcinus maenas*, in Willapa Bay, Washington, USA. Estuaries Coasts 29(6) (in press)
Mohamedeen H, Hartnoll RG (1989) Larval and postlarval growth of individually reared specimens of the common shore crab *Carcinus maenas* L. J Exp Mar Biol Ecol 134:1–24
Morgan SG (1995) Life and death in the plankton: larval mortality and adaptation. In: McEdward L (ed) Ecology of marine invertebrate larvae. CRC Press, New York, pp 279–321
Nagaraj M (1993) Combined effects of temperature and salinity on the zoeal development of the green crab, *Carcinus maenas* (Linnaeus, 1758) (Decapoda: Portunidae). Sci Mar 57:1–8
OTA, Office of Technology Assessment (1993) Harmful Non-indigenous Species in the United States. Report No. OTA-F-565, Office of Technology Assessment (US Congress), US Government Printing Office, Washington, DC
Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52:273–288
Queiroga H, Costlow JD, Moreira MH (1994) Larval abundance patterns of *Carcinus maenas* (Decapoda, Brachyura) in Canal de Mira (Ria de Aveiro, Portugal). Mar Ecol Prog Ser 111:63–72
Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. Annu Rev Ecol Syst 31:481–531
Sharpe PJH, DeMichele DW (1977) Reaction kinetics of poikilotherm development. J Theor Biol 64:649–670
Taylor F (1981) Ecology and evolution of physiological time in insects. Am Nat 117:1–23
Thresher R, Proctor C, Ruiz G, Gurney R, MacKinnon C, Walton W, Rodriguez L, Bax N (2003) Invasion dynamics of the European shore crab, *Carcinus maenas*, in Australia. Mar Biol 142:867–876
Wasson K, Zabin CJ, Bedinger L, Diaz MC, Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. Biol Conserv 102:143–153
Welch WR (1968) Changes in abundance of the green crab, *Carcinus maenas* (L.), in relation to recent temperature changes. Fish Bull US 67:337–345