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A mechanistic model for understanding invasions: Using the environment as a predictor of population success

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ABSTRACT

Aim: We set out to develop a temperature- and salinity-dependent mechanistic population model for copepods that can be used to understand the role of environmental parameters in population growth or decline. Models are an important tool for understanding the dynamics of invasive species; our model can be used to determine an organism's niche and explore the potential for invasion of a new habitat.

Location: Strait of Georgia, British Columbia, Canada.

Methods: We developed a birth rate model to determine the environmental niche for an estuarine copepod. We conducted laboratory experiments to estimate demographic parameters over a range of temperatures and salinities for *Eurytemora affinis* collected from the Nanaimo Estuary, British Columbia (BC). The parameterized model was then used to explore what environmental conditions resulted in population growth versus decline. We then re-parameterized our model using previously published data for *E. affinis* collected in the Seine Estuary, France (SE) and compared the dynamics of the two populations.

Results: We established regions in temperature-salinity space where *E. affinis* populations from BC would likely grow versus decline. In general, the population from BC exhibited positive and higher intrinsic growth rates at higher temperatures and salinities. The population from SE exhibited positive and higher growth rates with increasing temperature and decreasing salinity. These different relationships with environmental parameters resulted in predictions of complex interactions among temperature, salinity, and growth rates if the two sub-species inhabited the same estuary.

Main Conclusions: We developed a new mechanistic model that describes population dynamics in terms of temperature and salinity. This model may prove especially useful in predicting the potential for invasion by copepods transported to Pacific Northwest estuaries via ballast water, or in any system where an ecosystem is subject to invasion by a species that shares demographic characteristics with an established (sub)species.

Keywords: ballast water, Copepoda, estuarine, *Eurytemora affinis*, invasive species, mechanistic model, population dynamics

Running title: A model for invasive estuarine copepod populations

1 INTRODUCTION

Estuarine ecosystems are susceptible to invasions by planktonic non-indigenous species, primarily via ballast water discharges of commercial ships. Estuaries in the Northeast Pacific are particularly susceptible due to high ship traffic from Asia and among ports along the North American coast (Carlton 1987, Cordell and Morrison 1996, Cordell *et al.* 2008). Copepods are among the most abundant taxa found in ballast tanks (Smith *et al.* 1999, Cordell *et al.* 2009), accounting for more than 56.3% (96 of 176 taxa) of the total number of organisms found in ballast samples entering Vancouver Harbor (DiBacco *et al.* submitted). Furthermore, ballast release has been implicated as the source for several successful cases of invasive copepod establishment (Orsi and Ohtsuka 1999, Hirakawa 1988, Seuront 2005, Cordell *et al.* 2008). In some cases, these introductions may have contributed to displacement of native copepod species (Gubanova 2000, Horvath *et al.* 2001, Riccardi and Giussani 2007, Cordell *et al.* 2008), with potential consequences for higher levels of the food chain (e.g. Hobbs *et al.* 2006, Bryant and Arnold 2007).

A significant amount of research on invasive species has been devoted to risk assessment, or determining the potential for invasion of a particular habitat based on an array of factors such as ecology, economics, or physiology. Factors that have been considered include propagule pressure (Lockwood *et al.* 2005, Colautti *et al.* 2006), prior invasion success (Moyle and Marchetti 2006), diversity of the invaded habitat(Borrvall and Ebenman 2008), and similarity between native and introduced habitats (Carlton 1996). Many of the published studies are correlative in nature, using statistical approaches to find patterns consistent across invasive species. This approach is contrasted with a mechanistic approach, wherein data on functional traits are used to infer potential ranges (Kearney and Porter 2009). Correlative species distribution models are useful because they require minimal knowledge of the mechanistic links between the environment and the organism; this can be advantageous for species that are poorly studied. A disadvantage of such correlative studies is that their predictive power outside of the study environment is minimal (Davis *et al.* 1998). Many of the models used to predict invasion are ecological niche models (ENM) (reviewed in Guisan and Zimmermann 2000, Peterson 2003). ENM has gained attention recently as a potentially useful tool in the prediction of invasive species spread. Most uses of this type of model tend to rely on current species distributions combined with conditions in the invaded region to predict potential spread (e.g. Peterson and Vieglais 2001, Peterson and Robins 2003, Steiner *et al.* 2008), although more recently there have been examples of combining ENM and physiological parameters to predict invasion (Kearney and Porter 2004, Ebeling *et al.* 2008, Brown *et al.* 2008).

A mechanistic approach to understanding species distributions, which includes understanding the limitations of distribution and abundance, provides more robust data that can be extrapolated to new environments (Kearney and Porter 2009). In this study we develop a mechanistic model for copepod population dynamics as a function of environmental parameters. Both correlative and mechanistic approaches are useful for understanding invasibility but require different types and amounts of data. It is useful to compare results from both approaches, and in the case of invasive species, such comparisons may better determine the potential for successful invasion of a given habitat (Drake 2005).

It is widely argued that propagule pressure is among the most important factors in determining invasion success (Lockwood *et al.* 2005, Kolar and Lodge 2001). This includes number of individuals released and number of introduction attempts (both aspects of propagule pressure)

(Kolar and Lodge 2001). There are also characteristics that are common in groups of species that invade or spread, and therefore are also important for determining success. For instance, in fish species, there is increased probability of invasion success if the species has a history of successful invasion in other areas, high physiological tolerance, and a large number of propagules released (Moyle and Marchetti 2006). Other biotic factors that are often significantly associated with invasion success are adult size, size of native range, trophic status, and reduced biomass or diversity of native populations (Marchetti *et al*. 2004, Dzialowski *et al*. 2007).

Along with propagule pressure and species characteristics, environmental characteristics are among the most important factors in determining invasion success. In fact, Moyle and Light (1996) found that abiotic factors were more important than biotic factors for establishments of invasive fishes. In a meta-analysis of 49 studies, Hayes and Barry (2008) found that the only characteristic that was consistently significantly associated with successful invasion was a close match between the native and introduced habitats. This is because invasive species must be able to survive and reproduce in the invaded habitat.

Information on a species' demographic characteristics as a function of important environmental parameters would be useful in predicting its potential success as an invader (Ruesink *et al*. 1995). In most cases, there is no information available on intrinsic population growth rate as a function of environmental parameters for invasive species. Given a particular range of environmental parameters known to be important for population dynamics, a formula for calculating growth rate would allow researchers to estimate the risk of successful establishment for a given habitat. More interesting, perhaps, would be the comparison of population growth rates of native and invasive species, or among two or more invasive species. In this way it may be possible to explore processes such as competition and niche differentiation that affect species distributions.

Here we develop a mechanistic model for calculating population growth rate and net reproductive rate as a function of temperature and salinity for an estuarine copepod. The model requires information about the proportion of individuals moving into the adult stage over time, mortality rates, and fecundity. We parameterize the model using data collected on the calanoid copepod *Eurytemora affinis*, in a series of laboratory experiments. *E. affinis* is a species complex (Lee 2000, Lee and Frost 2002), occurring primarily in brackish environments. We found that over the range of temperatures and salinities tested, there is a zero-growth isocline in temperature-salinity space that demarcates where the population would be able to grow, and where it would decline to zero. We then reparameterized the model using previously published data on a separate clade of *E. affinis* from the Seine Estuary, France (Devreker *et al*. 2007, 2009). We were then able to compare mechanistic niches for the two clades of *E. affinis*. This serves to illustrate the utility of the model for predicting which (sub)species would likely dominate a given environmental niche based on the effects of abiotic factors on population growth rate. Model results for the single species case show that, given data on the relationship between environmental parameters and demographic parameters, regions of population growth or decline can be determined. Model results from comparing two (sub)species may provide insight into interactions between environmental (temperature and salinity) and biological (i.e. population growth rate) factors that influence species presence/absence. This may be an especially useful tool in studies where an invasive organism has the potential to displace a native species that occupies a similar niche.

Eurytemora affinis is a dominant organism in many temperate estuaries. The species complex has the most eurytolerant members of its genus, occupying habitats with salinities that range from fresh to full strength seawater (Heron 1976). *E. affinis* is an important component of the estuarine food web (Koski *et al*. 1999, Tackx *et al*. 2003, Reaugh *et al*. 2007), including its role as a food source for higher trophic levels (Hardy 1924, Meng and Orsi 1991, Winkler and Greve 2004). The ubiquity of *E. affinis* in the marine environment, and its recent invasion to fresh water (Lee 1999, Lee and Bell 1999, and references therein), make it an ideal model organism to examine how temperature and salinity affect population dynamics in the laboratory.

Eurytemora affinis is also an interesting organism for our study because of the extensive work that has been conducted on the species complex's ability to adapt to novel habitats and tolerate different salinity regimes. Although the species complex is capable of inhabiting a wide range of salinities, Lee *et al*. (2003) showed that there are tradeoffs associated with a population evolving in high- versus low-salinity environments. We can therefore assume that, in an estuary where an individual experiences a range of environmental conditions, that individual will maximize its time in the habitat for which it is most evolutionarily suited. Furthermore, using laboratory experiments where *E. affinis* was reared over multiple generations at a range of salinities, Lee *et al*. (2007) provided evidence that *E. affinis* populations adapted to a range of salinities have sufficient levels of genetic variation for fitness-related traits upon which selection could act, thereby affecting their ability to invade. Natural selection therefore plays an important role in determining *E. affinis*' ability to survive and reproduce in a particular salinity regime (Lee and Petersen 2003).

There have been several laboratory studies examining the effects of temperature and salinity on *E. affinis* specific demographic parameters, including development time (Vuorinen 1982, Nagaraj 1988, Ban 1994) and egg production (Ban 1994, Andersen and Nielsen 1997, Hirche 1992, Devreker *et al*. 2009), however none of these previous studies examine the effects of temperature and salinity on population growth rate explicitly. Here we collected data on multiple population parameters for the purposes of determining the overall effects of temperature and salinity on the population via calculation of population growth rate.

2 METHODS

2.1 Population Model

We used the Lotka Integral Equation to model the copepod birth rate; Lotka's model is a continuous-time equation that tracks birth rates over continuous time for an age (or stage) structured population (Sharpe and Lotka 1911, Lotka 1939):

$$B(t) = \int_0^\infty B(t-a)l(a)m(a)da + G(t) \tag{1}$$

where $B(t)dt$ is the number of female births in the time (t) interval t to $t + dt$, $l(a)$ is the fraction of new-born females surviving to age a, and $m(a)$ is the rate of production of females by females of age a. $G(t)$ is the contribution of all females already present at $t = 0$; our model was structured such that $G(t) = 0$. To solve (1), we directly substitute $B(t) = Qe^{rt}$, which gives the Euler-Lotka equation:

$$1 = \int_0^\infty e^{-ra}l(a)m(a)da \tag{2}$$

If we define the function $\psi(r)$ to be

$$\psi(r) \equiv \int_0^\infty e^{-ra} l(a) m(a) da \tag{3}$$

we can write the characteristic equation as $\psi(r)$. There is exactly one real root r^* that solves (2), giving the growth rate of the population. The net reproductive rate R_0, which is the mean number of offspring per individual over its lifetime (Caswell 2001), occurs where $\psi(r)$ crosses the ordinate:

$$R_0 \equiv \psi(0) = \int_0^\infty l(a) m(a) da \tag{4}$$

We can therefore obtain the population growth rate r^* and net reproductive rate R_0 by substituting appropriate equations for $l(a)$ and $m(a)$ into (2) and (4). The benefit of calculating the intrinsic rate of population increase, r, is that it integrates age at first reproduction, survivorship, brood size and frequency, and longevity into a single statistic.

For *Eurytemora affinis*,

$l(a) = e^{-\mu a}$ where μ is mortality rate
$m(a) = \beta \times G(a;b,k)$ where β is fecundity (eggs × adult female^{-1} × time^{-1})
$G(a;b,k) =$ gamma cumulative distribution function with parameters b, k

(see Sections 2.3.1-2.3.3). Given that k is an integer, the gamma cumulative distribution function simplifies to

$$G(a;b,k) = 1 - \sum_{i=0}^{k-1} \frac{a^i b^{-i}}{i!} e^{(-a/b)}. \tag{5}$$

By substituting and simplifying, (2) becomes

$$1 = \frac{\beta}{r+\mu} - \beta \sum_{i=0}^{k-1} \frac{b^{-i}}{i!} \int_0^\infty a^i e^{-(r+\mu+1/b)a} da. \tag{6}$$

The integral in (6) can be solved using integration by parts, such that

$$\int_0^\infty a^i e^{-(r+\mu+1/b)a} da = \frac{i!}{(r+\mu+1/b)^{i+1}}. \tag{7}$$

Substituting (7) into (6) yields

$$\begin{aligned} 1 &= \frac{\beta}{r+\mu} - \beta \sum_{i=0}^{k-1} \frac{b^{-i}}{i!} \frac{i!}{(r+\mu+1/b)^{i+1}} \\ &= b\beta \left(\frac{1}{b(r+\mu)} - \sum_{j=1}^{k} \frac{1}{(br+b\mu+1)^j} \right) \text{ where } j = i+1 \end{aligned} \tag{8}$$

This can be numerically solved for the population growth rate, r.

2.2 Experiments

2.2.1 Laboratory Setup and Algae Culturing

Experiments were conducted at the Centre for Aquaculture and Environmental Research, Fisheries and Oceans Canada, West Vancouver, British Columbia. Seawater (32 psu) and creek water (0 psu) were pumped from nearby sources to the laboratory facility and filtered to remove particles >1 µm; brackish salinities used in the experiment were achieved by mixing seawater and creek water. We chose natural seawater and freshwater because they are more likely to mimic natural conditions. This does, however, introduce the possibility factors other than salinity differing among treatments, such as trace metals, pollutants, or other dissolved chemicals. Two large incubators (5°C and 10°C) and one cold room (15°C) were used to maintain experimental temperatures. Temperature loggers were used throughout the experiments to verify that environmental conditions were stable. Incubators and the cold room were kept on 12-hour light/dark cycles.

The marine green alga *Tetrasalmis suecia* was cultured as food for all stages of *Eurytemora affinis*. *T. suecia* has a high lipid level and is mobile, therefore it is easily grown in a laboratory setting. Preliminary experiments showed that *T. suecia* fluorescence was unaffected by transfer from higher to lower salinity waters and vice versa, without acclimation periods, suggesting cells were not compromised by salinity changes. A high tolerance to salinity changes was important since the same algal stocks were used to feed copepods at salinities ranging from 4 to 12 psu. *T. suecia* was therefore cultured at 12 psu and added directly to copepod cultures irrespective of salinity conditions. The stock culture was kept at 15°C.

2.2.2 Broodstock Collection and Processing

Eurytemora affinis adults were collected during high tide on two dates in September 2009 from the Nanaimo River Estuary on Vancouver Island, British Columbia (49° 7'49.3"N, 123° 53' 35.9"W). Previous surveys showed *E. affinis* to be abundant in this location (Cordell and Morrison 1996). Water temperature was approximately 16°C and salinity ranged from 3 to 8 psu over the course of the one hour collection periods. A 250 µm plankton net with a 0.5 m diameter opening was pulled horizontally by hand in 1-1.5 m deep water for approximately 10 m. Net contents were then rinsed into jars using estuary water and stored in a cooler for transport back to the laboratory.

Field samples were stored at 15°C until processed. Samples were first sieved to remove material >2 mm. The remaining material was placed in a 500 ml beaker with 12 psu 15°C seawater. Organic matter and non-copepod macroinvertebrates were removed via pipette from field samples after 2-3 hours of settling time. Collections were stored overnight at 15°C; the following day any remaining organic matter and non-copepod macroinvertebrates were removed via pipette. Beaker contents were transferred to 500 ml plastic beakers with 200 µm mesh bottoms, nested inside solid-bottomed beakers, containing filtered 12 psu seawater and *Tetrasalmis suecia* at 8×10^4 cells ml^{-1}. The mesh retained adult-sized copepods but allowed naupliar and early copepodite stages to pass through to the bottom beaker.

Adult copepods from several beakers were collected and examined under a dissecting microscope to confirm the exclusive presence of *Eurytemora affinis*. In all cases, no species other than *E. affinis* were found. Species identification was made using Katona (1971). Photographs were taken of several *E. affinis* individuals and sent to J. Cordell (University of Washington) for further species confirmation. Lengths of individuals collected ranged from 400-800 µm with a 1:1 sex ratio.

After three days in the laboratory setting, all beakers contained newly hatched nauplii, indicating that conditions were suitable for copepod viability. Adults were mixed and divided into one of the nine treatment combinations of three temperatures (5°, 10°, 15°C) crossed with three salinities (4, 8, 12 psu). Nauplii produced in the first week after transfer to new salinity and temperature conditions were not used for experiments; they were removed from beakers and cultured for use as future broodstock.

2.2.3 Experimental Setup

After the initial week of broodstock acclimation, newly hatched nauplii were collected from broodstock beakers daily for experimental use. Nauplii from multiple beakers of the same treatment conditions were combined and the number of nauplii was estimated by subsampling a small volume and counting the number of individuals present. Nauplii for each treatment were then divided into one of three 500 ml replicate beakers comprised of an internal beaker with a 50 µm mesh bottom nested in a solid-bottom beaker. *Tetrasalmis suecia* was added at a concentration of approximately 8×10^4 cells ml^{-1} .

Copepods were reared from the first naupliar stage under treatment conditions. When all individuals were past the copepodite IV stage, the interior beaker mesh was changed to 150 µm. This allowed late stage copepodites and adults to be retained while facilitating removal of any newly hatched nauplii. Individuals in beakers were counted and their stages noted every two days for 60 days or until there were no live copepods remaining. Counting and staging involved estimating 1) the proportion of individuals in each developmental stage, 2) population size, and 3) the number of newly hatched nauplii. The proportion of individuals in each stage was estimated by subsampling beaker contents and examining five haphazardly chosen individuals under both a dissecting and a compound microscope. Stage identifications were made using Katona (1971). Subsampled individuals tended to be of the same stage, especially earlier in the experiment. Population size was estimated by averaging the number of copepods in five 1-ml samples to obtain the average number of individuals per ml. This average was then used to extrapolate back to the entire population by multiplying by the beaker volume. Once females began producing nauplii, the number produced was estimated in the same way. Nauplii were removed from experimental beakers after counting so that only the original population was assessed for population size and proportion in each stage.

2.3 Parameter Estimation

We estimated the relationship between parameters associated with maturation rate, mortality rate, and fecundity, and temperature and salinity (details below). These rates were assumed to have a quadratic relationship with both temperature and salinity: there is an optimum value for both temperature and salinity above and below which rates should result in slower population growth. We therefore fit our data to a model with quadratic terms for each of the parameters estimated of the form

$$\theta(T,S) = \tau_0 + \tau_1 T + \tau_2 S + \tau_3 TS + \tau_4 T^2 + \tau_5 S^2 \tag{9}$$

After fitting the model to the data, we then systematically removed terms and compared the resulting models using F-tests. All models included the $\tau_1 T$ and $\tau_2 T$ terms; of the remaining terms only those that significantly affected the fit were kept.

2.3.1 Maturation Rate

Previous studies have shown that a gamma distribution best describes the expected proportion of individuals in a given stage over time for copepods (Manly 1988, Klein-Breteler *et al*. 1994, Souissi *et al*. 1997). The gamma distribution is traditionally used for “waiting times”, that is, events (such as moving to a new stage) that occur with some probability following a binomial distribution. We therefore assumed stage duration followed a gamma distribution with a scale parameter *b* and a shape parameter *k*. To calculate maturation rate for our model, we are only interested in the proportion of individuals that pass from the last copepodite stage (the copepodite V, hereafter CV, stage) into adulthood. We therefore only needed *b* and *k* parameters for the CV stage. The important parameters for the Lotka Integral Equation model is the probability of surviving to reproduce, and given that you do, the fecundity. Therefore we are mapping directly to the adult stage, rather than describing the intervening stages. This means effects of mortality rate are not included in maturate rate estimates.

We used the additive property of probability distributions to estimate *b* and *k* from our measurements. The additive property states that, if the time to develop to the first stage follows a gamma distribution, and the duration of each stage is independently gamma distributed, then the time of development to each stage will also follow a gamma distribution (Kempton 1979). The data we collected in the laboratory were the proportion of the population that has yet to pass through the CV stage, which implies that over the course of the experiment our data set begins at 1 and declines to 0. Since the gamma distribution over stages is additive and stage development is unidirectional, our data are cumulative and follow one minus the cumulative gamma distribution function.

We used maximum likelihood to estimate *b* and *k* based on the proportion of individuals that had reached the adult stage over time (x_i). The cumulative gamma distribution function can be simplified if *k* is a positive integer, as it is here, to

$$F(x;k,b) = 1 - \sum_{i=1}^{k-1} \frac{xb^i}{i!} e^{-xb}$$

To estimate *b* and *k*, we are interested in one minus the cumulative gamma distribution function, which we denote as π:

$$\pi_i = 1 - F(x;k,b). \tag{10}$$

The log likelihood equation used to estimate *b* and *k* is therefore

$$\log L = -\sum_{i=1}^{T} [(1 - x_i)\log(1 - \pi_i) + (x_i)\log(\pi_i)]. \tag{11}$$

We estimated *b* and *k* for each replicate beaker and used the resulting outputs to estimate coefficients for equations expressing the relationship between *b* and *k* and temperature and salinity via nonlinear least squares (*nls* in the R programming language):

$$\begin{aligned} b &= f(T,S) \\ &= \exp(b_0 + b_1 T + b_2 S + b_3 TS) \qquad (12) \\ k &= f(T,S) \\ &= \exp(k_0 + k_1 T + k_2 S + k_3 TS) \qquad (13) \end{aligned}$$

The exponential form of these equations forces estimates of *b* and *k* to be > 0.
Maturation rates can be calculated from *b* and *k* since duration time $d = b \times k$. Maturation rate into adulthood is then

$$\delta = \frac{1}{d}. \qquad (14)$$

Time constraints prevented us from assessing sex and stage for all experimental individuals at each time step. We therefore assumed that mortality rate is constant across stages, and were not able to ascertain its effects on maturation rate.

2.3.2 Mortality Rate

Mortality rates were estimated from population size estimates over time. Nauplii produced by females in experimental treatments were removed within 48 hours of production. As a result, copepod populations in each beaker underwent a pure death process (i.e. no individuals joined the population during the experiment). Population decline over time can therefore be used directly to estimate mortality rates. Time constraints limited our ability to obtain stage-specific population size estimates, therefore mortality rate was estimated for the entire population regardless of stage. Population size estimates for each beaker over time (*N(t)*) were first normalized to the largest size estimated in that beaker over the course of the experiments to give $\tilde{N}(t)$. This value was always the size estimated at t=1. This was necessary since starting population sizes were not equal among beakers (although densities were consistently below those reported in other experiments on *E. affinis*; see Ban (1994) and Devreker *et al*. (2007)). Normalized size data were then log transformed and a linear decline over time was assumed.

We used a linear model (implemented in R using the *lm* command) to estimate coefficients for the relationship between population size, time, temperature, and salinity:

$$\ln \tilde{N}(t) = (c_0 + c_1 S + c_2 T + c_3 S^2 + c_4 T^2) \times t. \qquad (15)$$

Each population declined over time from their normalized value of $\tilde{N}(t) = 1$, therefore the y-intercept was assumed to be zero since $\ln(1) = 0$. From this equation it follows that mortality rate μ is

$$\begin{aligned} \mu &= f(T,S) \\ &= c_0 + c_1 S + c_2 T + c_3 S^2 + c_4 T^2. \qquad (16) \end{aligned}$$

2.3.3 Fecundity

Fecundity (β) was estimated for adult females using population size estimates, the proportion of adults at a given time step, the assumption of a 1:1 sex ratio, and the number of nauplii produced per time step. The equation used to calculate fecundity was

$$\beta = \frac{n_n}{n_T \times a \times 0.5} \tag{17}$$

where n_n is the estimated number of newly produced nauplii, n_T is estimated population size (excluding newly produced nauplii), and a is the proportion of adults in the population (estimated number of adults divided by estimated population size). β was calculated for each time step in each replicate beaker where adult females successfully produced nauplii. We assumed no Allee effects (no mate limitation) and no senescence (all adult females were capable of reproduction). These are valid assumptions since there were always adult males present and culture volume was not prohibitively large, and because there is no evidence of senescence in copepods. We used nonlinear least squares to estimate coefficients for an equation expressing β as a function of temperature and salinity:

$$\begin{aligned}\beta &= f(T,S)\\ &= \exp(f_0 + f_1 T + f_2 S + f_3 TS).\end{aligned} \tag{18}$$

The exponential form forces estimates of β to be > 0.

2.4 Comparing two populations

One potential use for our model is for comparing population growth rates across environmental parameters for two or more species or subspecies. To illustrate this, we calculated parameters for the population model (8) using previously published data for *E. affinis* collected in the Seine Estuary, France (Devreker et al. 2007, 2009). The raw data consisted of reproduction, percent survival, and stage duration for *E. affinis* reared in the laboratory at two temperatures (10°, 15°C) and three salinities (5, 15, 25 psu). A complete data set was not available for the 10°C 25 psu treatment because individuals did not survive and mature past the copepodite III stage.

We estimated b and k parameters for the cumulative gamma distribution in (11) based on published values of parameters for the gamma distribution function describing development from the naupliar I stage to the CV stage (Devreker *et al*. 2007, Table 3). We then estimated coefficients for (12)-(13) to obtain b and k as functions of temperature and salinity. We used reported values for percent mortality in Devreker *et al*. (2009, Table 1) to estimate coefficients for μ as a function of temperature and salinity according to

$$\mu(T,S) = \exp(m_1 + m_2 S + m_3 T + m_4 ST). \tag{19}$$

The exponential form forces estimates of μ to be > 0. We calculated coefficients for β according to (18) using published values for mean egg production rate from Devreker *et al*. (2009, Table 1), which is equivalent to fecundity.

Parameter estimates for (12)-(13), (19), and (18) were then used to calculate b, k, μ and β respectively for the Seine Estuary population of *Eurytemora affinis* over a range of temperatures and salinities. We then calculated population growth rate for the population using (8).

3 RESULTS

3.1 Experiment Summary

Eurytemora affinis individuals in the 10° C and 15° C temperature treatments developed through its 12 documented stages with varying stage durations (Katona 1971, Vijverberg 1980). At 15°C, copepods completed their life cycles within the 60 day experimental period, with life spans of approximately 40, 54, and 54 days for individuals in salinities 4, 8, and 12 psu, respectively. Copepods in the 10°C treatments had longer life spans than those in the 15°C treatments; individuals in the 4 psu treatment had life spans of approximately 55 days, while many individuals in the 8 and 12 psu treatments were still viable when the experiment was terminated at 61 days. Individuals in the 5° C treatments did not develop past the first two copepodite stages during the experimental period. As a result, life spans were longer than the length of the experimental period. This result is consistent with previously published studies of *E. affinis* reared at cold temperatures (Katona 1970, Heinle and Flemer 1975).

3.2 Parameter Estimation

3.2.1 Maturation Rate

Maturation rates were not explicitly estimated; rather, the parameters b and k associated with the cumulative gamma distribution in (11) were estimated for the CV stage. These estimates were then used to calculate population growth rate and net reproduction rate using (8). Temperature significantly affected k, however no other significant relationships to temperature and salinity were detected (Table 1). Coefficient estimates for b and k equations (12)-(13) are given in Table 2 and their relationship to temperature and salinity were plotted (Fig. 1).

We calculated maturation rate, δ, as a function of temperature and salinity using b and k estimates and (14) (Fig. 2). Although maturation rate was not explicitly calculated as a function of temperature, in general observations suggested that maturation rates and generation times were positively correlated with temperature. These observations are in agreement with previously published studies of *E. affinis* (Katona 1970, Ban 1994, Devreker *et al*. 2004, 2007).

3.2.2 Mortality Rate

Salinity and temperature were both shown to significantly affect mortality rate in our experiments (Table 3). Mortality rate as a function of temperature and salinity was estimated based on exponential declines in population size according to (15). In general, mortality rate tended to increase as temperature increased and salinity decreased (Fig. 3(a)). Coefficients for (16) are given in Table 2.

Fecundity

Fecundity was estimated for each of the treatments according to (17). We found that temperature, and the interaction between temperature and salinity, significantly affected fecundity (Table 3). Nonlinear least squares was used to estimate coefficients for (18) (Table 2). In general, fecundity tended to increase with temperature and salinity (Fig. 3(b)).

Model Analysis

Single population

Numerical methods were used to calculate population growth rate r and net reproductive rate R_0 according to (8). We used temperature- and salinity-dependent estimates of b, k, μ, and β to parameterize the model, so that r and R_0 were a function of temperature and salinity. We plotted the results for the range of temperatures and salinities from our experiments (5°C to 15°C and 4 to 12 psu) (Fig. 4). In general, *E. affinis* populations decline ($r < 0$) at lower temperatures and salinities and increase ($r > 0$) at higher temperatures and salinities. Increases in either temperature or salinity result in increases in r, therefore interactions between the two also increase growth rate. The line of zero growth runs diagonally across the temperature-salinity plane from 10°C, 4 psu to 5°C, 7.5 psu. Below this line, the population would decline over time, while above it, the population would increase. Results for R_0 mirror those of r (not shown).

Our calculation of r is in agreement with previously published values of r for *E. affinis*: Daniels and Allan (1981) reported that at 18°C and 8-10 psu, *E. affinis* had an intrinsic growth rate of approximately 0.18. Using our equations to estimate r at this temperature and salinity results in comparable values, with r ranging from 0.21 to 0.24 (for 10 and 8 psu, respectively).

Comparing two populations

We estimated parameters for (12)-(13), (19) and (18) for the Seine Estuary population of *Eurytemora affinis* (Table 4). We then calculated b, k, μ and β respectively over a range of temperatures and salinities to estimate population growth rate for the population using (8).

When comparing *E. affinis* populations from Nanaimo Estuary, British Columbia (BC) and Seine Estuary, France (SE), growth rate increased rapidly with increasing temperature for the SE population, but was less affected by salinity compared to the BC population (Fig. 5). To directly compare growth rates, we calculated the lines of zero growth for both populations and illustrated whether populations were growing or declining given a particular point in the temperature-salinity space (Fig. 6). At low temperatures and salinities, both BC and SE populations would decline over time. SE has a negative growth rate at lower temperatures, however this effect is mitigated slightly with decreasing temperature. In contrast, BC has a positive growth rate above 10°C and 7.5 psu. As a result, at low temperatures and high salinities BC is growing while SE is declining. There is a small window at intermediate temperatures and low salinities where BC is declining and the SE is growing. In the region where both BC and SE are growing, at lower salinities SE tends to grow faster than BC (shaded region in Fig. 6) while at high salinities BC grows faster. This result can be interpreted as suggesting that at lower salinities and higher temperatures, SE would dominate a habitat shared with BC due to higher growth rates, while at higher salinities BC would dominate.

4 DISCUSSION

In this study, we used a birth rate model to determine the environmental niche for an estuarine copepod in terms of salinity and temperature. We then expanded the model application to compare growth rates of two (sub)species that may share the same environment. Such an application may be useful as a tool for predicting the outcomes of invasive species moving into a habitat already occupied by a similar native species. Given information on transitions to the CV stage, fecundity, and mortality, we can use this model to predict which of the copepod taxa arriving in ballast tanks is most likely to establish and potentially displace native copepods. Our mortality estimate is effective mortality rate for the population, and is not broken into pre-adult and post-adult mortality. It is possible (or even likely) that the pre-reproduction mortality rate and post-reproduction mortality rates are different. We haven't investigated this, instead choosing primarily to focus on the effects of environmental conditions on the rates.

The Lotka Integral equation is a continuous time analogue to the more familiar discrete-time Leslie matrix model (Kot 2001). It is better suited than the commonly used Leslie Matrix model (Ch. 2, Caswell 2001) to the question at hand because growth and reproduction occur continually over the experiment. The Life Table Response Experiment approach (e.g. Caswell 1989) is an analytical process that decomposes contributions of environmental factors to the matrix population growth rate in a linear manner, analogous to the standard ANOVA for linear models. In our system, the population dynamics depend in a nonlinear fashion on temperature and salinity and parameterize these nonlinear functional relationships directly.

Ours is one of the few copepod models that determine population growth rate as a function of temperature and salinity. One notable exception is George (1985), who reported on the influence of temperature and salinity on *Eurytemora herdmani*, a conspecific of *E. affinis*. George found both linear and second order effects of temperature and salinity, in addition to interactions between them. Her equation for population growth rate, which indicates that optimum conditions are at 25 psu and 13°C, was

$$r = -0.609 + 0.059T - 0.002T^2 + 0.24S - 0.0004S^2 - 0.0003ST \tag{20}$$

which corresponded very closely with the relationship reported here. The benefit of calculating the population growth rate is that it integrates age at first reproduction, survivorship, brood size and frequency, and longevity into a single statistic while still retaining the ability to discriminate the relative significance of environmental parameters (e.g., salinity, temperature) on growth rates. Population growth rate can also be integrated easily into the invasive species framework since probability of establishment is positively correlated with higher rates of population growth (Lawton and Brown 1986, Drake and Lodge 2005). High population growth rates, like high propagule pressure, can allow a population quickly to escape the low numbers at which extinction is likely (Ruesink *et al.* 1995), although this is not a guarantee of invasion success and many contrary examples exist (Hayes and Barry 2008).

Both temperature and salinity have the ability to affect reproduction, growth, and mortality rates; it is not surprising that their interactive effects can also affect population growth rate. Devreker *et al.* (2009) found that a combination of low temperature and high salinities resulted in negative impacts on reproductive parameters for *E. affinis*. This effect was not seen in our study, likely because their study encompassed higher salinities. Nagaraj (1988) found that *Eurytemora velox* populations exhibited lower mortality rates at combinations of either higher temperatures and lower salinities, or lower temperatures and higher salinities, suggesting some interaction between the extremes of either factor result in increased mortality. With relation to tolerance to extremes, studies have demonstrated a temperature-salinity interaction effect on both salinity and temperature tolerance in crustaceans, such that temperature could affect optimal salinity (Bradley 1975). Furthermore, Kinne (1964) found that resistance to temperature extremes increased with salinity. Other studies have found an increase in upper lethal temperature with increases in salinity for lobster (McLeese 1956) and copepods (Remane and Schlieper 1971). In general, studies show an increase in temperature tolerance with increasing salinity, at least in the range below stressful salinities.

Calculating population growth rate as a function of temperature and salinity constitutes a mechanistic model of a population. Mechanistic models take into account the interactions between organisms and their environment; in our case, the "environment" is represented by temperature and salinity. Often mechanistic models are cited as an alternative to correlative models, which estimate the species' preferred environment using statistical procedures based on its known occurrences (Buckley *et al*. 2010). Mechanistic approaches are typically considered more difficult due to the large amount of physiological data needed to assess a species' niche, however such studies provide more explanatory power (Kearney and Porter 2004, Chamaille-Jammes *et al*. 2006) and are better at predicting range expansions (Buckley *et al*. 2010). More useful than mechanistic and correlative models alone is to combine the two approaches, especially since we do not always have the large amounts of information about species that is needed for effective mechanistic models (Buckley *et al*. 2010). Using our model to predict population growth rates in temperature-salinity space for a single species would complement a statistical model that uses knowledge from the known occurrences of the species to predict success in a new habitat. One of the most useful applications of a modeling approach that combines correlative and mechanistic methods would be in invasive species studies. Often correlative models are used to determine the potential for a particular habitat to be invaded (e.g. Moyle and Marchetti 2006, Borrvall and Ebenman 2008). If such models can be combined with mechanistic models like the one presented here, better estimates of invasibility might be possible (Kearney and Porter 2009).

We applied our mechanistic model to compare the population growth rates of two subspecies of *Eurytemora affinis* over a range of environmental conditions. It is not likely that the two subspecies we compared here will simultaneously encounter the same habitat, however there are incidences where different clades of the same species have invaded. For example, there is evidence that an Atlantic clade of the *E. affinis* species complex has recently invaded the northeast Pacific (Lee 2000, Winkler *et al*. 2008). Lee and Frost (2002) found evidence of morphological stasis of secondary sexual characteristics within North American clades of the *E. affinis* species complex, suggesting that such an invasion would be difficult to detect but have the potential to significantly affect demographic characteristics of populations.

Invasion by a subspecies are ecologically important considerations since the invading clade might have different potential physiological tolerances and therefore have the potential for spread into new habitats not previously inhabited by the native clade. Although this is not a traditional definition of species invasion Valéry *et al*. 2008), it constitutes range expansion and can result in a species moving into environments it did not previously inhabit. This type of invasion has received more attention recently, the best example being the cryptic invasion of species of the non-native common reed *Phragmites* in North America (Saltonstall 2002).

Although the *Eurytemora affinis* species complex is capable of inhabiting a wide range of salinities, experiments in Lee *et al*. (2003) indicated tradeoffs associated with a population evolving in a high- versus low-salinity environment. We can therefore assume that an individual experiencing an estuarine habitat with a range of potential salinities and temperatures, that individual will maximize its time in the habitat for which it is most evolutionarily suited. Here we tested salinities commonly found within the Nanaimo Estuary, and therefore expect that our experimental salinities are within the range of salinities for which this particular *E. affinis* population is evolutionarily adapted.

It is difficult to compare our results to those that might be observed in the field, primarily due to the nature of copepods in estuaries. Unlike in our laboratory experiments, copepods in nature have the ability to alter their surroundings by relocating: if temperatures or salinities become less than ideal, they are capable of moving up or down the gradient to more favorable conditions. We tested salinities commonly found within the Nanaimo Estuary, and therefore expect that our experimental salinities are within the range for which this particular *E. affinis* population is evolutionarily adapted (Lee *et al*. 2003, Lee and Petersen 2003). It is possible that our experimental conditions did not include the preferred temperatures at which these copepods live and reproduce, in which case growth rates we estimated might not be readily observed in nature. Although our experimental design forfeited some level of reality, the results are important contributions to our understanding of how copepod population growth varies with environmental conditions. There are no known field observations of estuarine copepod population growth rates, therefore it is difficult to ascertain whether there are significant differences in nature compared to our laboratory studies. Although the absolute values of growth rates calculated might be of limited use, we can expect that the relationships between growth rate and temperature and salinity are reliable.

One possible future application of our model is to explore the potential for invasive copepod establishment in the Fraser River and other rivers in British Columbia via ballast release. Several species of estuarine copepods from Asia have successfully established in the Columbia-Snake River system and in the Sacramento-San Joaquin estuary in the last 20 years (Orsi and Walter 1991, Cordell *et al*. 1992, 2008), likely as a result of transport in ballast tanks. Increases in population size of these species, namely *Pseudodiaptomus forbesi* and *P. inopinus*, coincided with reduced population size of the native species of copepods, including *Eurytemora affinis* (Orsi and Walter 1991, Meng and Orsi 1991). There are high volumes of ship traffic traveling among the ports in the northeast Pacific, with limited ballast exchange between stops Cordell *et al*. 2009, Lawrence and Cordell 2010). Despite high propagule pressure in ballast tanks (Cordell *et al*. 2008), neither *P. forbesi* nor *P. inopinus* have established in British Columbia waters (Bollens *et al*. 2002, Cordell *et al*. 2010). One way to explore the potential for their invasion or to establish the reason why they have yet to invade is using our mechanistic model, parameterized for *P. forbesi* and *P. inopinus*, and compare results to native species of copepods from BC, such as *E. affinis*. The role of competition in predicting the outcome of invasions is not well studied, primarily because of the difficulty associated with teasing apart biotic and abiotic effects (but see Riccardi and Giussani 2007). Comparing population growth rates among these species over the range of temperatures and salinities relevant to BC waters might shed some light on whether the physical factors are impeding invasion, or whether there might be biotic factors at play.

There are several ways that a non-indigenous species might invade; scenarios might include introduction via anthropogenic causes such as ballast release or rapid evolutionary events that allow the species to move into environments previously uninhabitable due to physiological constraints. Our model is likely more useful for some of these scenarios than others. For instance, rapid evolutionary shifts would be difficult to predict using our mechanistic model. If such shifts take place over several generations, however, laboratory studies might reveal enough information about the process to allow for prediction of invasion potential using a model such as ours, modified to include tolerance shifts. The model presented here is more useful in cases where invasion is anthropogenically caused, since conditions of the new environment can be compared to the potential for population growth in a given temperature and salinity range.

The model presented here should be considered another useful tool for predicting invasive species spread; many other models have been developed that may be more useful in a given situation, or may supplement information gained from using our model. ENM are one such type of model, wherein occurrence data for a species' native range is used to determine the possibility of spread in the invaded habitat. Another category of model used to determine the potential for species invasion is linear models, including logistic regression (e.g. Buchan and Padilla 2000, Allen and Ramcharan 2001), multiple regression (e.g. Marchetti *et al*. 2004, Jones and Ricciardi 2005), and discriminant function analysis combined with gravity models (MacIsaac *et al*. 2004). These models are limited by the fact that some input variables are not independent of one another, or effects considered in the model are additive (Olden and Jackson 2002). Nonlinear and nonparametric models (including ENM) do not have this limitation, but are more complex and potentially include correlations that are not useful in predicting a species' future distribution under novel circumstances, such as global warming (Davis *et al*. 1998). Perhaps the most useful approach is to combine the many tools available to take advantage of the strengths of each. An exemplary study where this approach was used is Cordell *et al*. (2010), wherein parametric, linear approaches and nonparametric, non-linear techniques were used to explore invasion by *Pseudodiaptomus inopinus*.

Population biology can play an important role in studies of invasive species via life history studies and demographic models (Sakai *et al*. 2001). Mechanistic models that explore the relationship between physiology and the environment (such as the one presented here) have the potential to play critical roles in understanding invasions and spread in the marine environment. This is especially true if their predictive power is combined with correlative models that better incorporate multiple and disparate factors influencing spread.

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Biosketch: The authors of this paper are part of the Canadian Aquatic Invasive Species Network (CAISN, www.caisn.ca), which is a consortium of scientists who are interested in identifying and examining aquatic invasions. One of the objectives of CAISN is to study the principle vectors and pathways that transport aquatic invasive species into Canadian ecosystems; our study fits into this objective. MAL and CD conceived the idea for this project as a result of interactions via CAISN activities. CAS conducted experiments, performed analyses, and led the writing; MAL contributed to conceptualizing the model and its analysis; CD contributed to experiment design, model interpretation, and writing.

CA Strasser, MA Lewis, and C DiBacco. 2011. A mechanistic model for understanding invasions: Using the environment as a predictor of population success. Diversity and Distributions 17:1210-1224. doi:10.1111/j.1472-4642.2011.00791.x.

Table 1. Results from ANOVA for *b* and *k*. Significant F values at the $\alpha = 0.05$ level are indicated with *. *k* values were log(x+1) transformed to meet ANOVA assumptions of normality and homogeneity of variance prior to analysis.

		b			*k*		
Source	d.f.	MS	F	p	MS	F	p
S	2	0.030	0.22	0.805	91	1.10	0.364
T	1	0.552	4.01	0.069	1911	22.93	<0.0005*
S × T	2	0.253	1.83	0.202	148	1.78	0.210
Error	12	0.138			83		

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Table 2. Coefficient estimates for (12)-(13), (16), and (18). Coefficients that are significant at the $p = 0.05$ level are indicated with *.

Parameter	Coefficient	Estimate	p
Maturation, *b*	b_0	1.57	0.309
	b_1	-3.83×10^{-1}	0.081
	b_2	-1.37×10^{-1}	0.245
	b_3	2.92×10^{-2}	0.067
Maturation, *k*	k_0	3.51	0.028^*
	k_1	2.38×10^{-1}	0.186
	k_2	-4.60×10^{-2}	0.727
	k_3	-1.84×10^{-2}	0.267
Mortality	c_0	-1.65×10^{-2}	$<0.0001^*$
	c_1	1.10×10^{-2}	0.0002^*
	c_2	-2.59×10^{-3}	0.230
	c_3	-3.45×10^{-4}	0.047^*
	c_4	-3.26×10^{-4}	0.002^*
Fecundity	f_0	-2.56	0.076
	f_1	3.60×10^{-1}	0.007^*
	f_2	2.85×10^{-1}	0.005^*
	f_3	-2.40×10^{-2}	0.01^*

Table 3. Results from ANOVA for μ and β. Significant F values at the $\alpha = 0.05$ level are indicated with *. μ and β values were log(x+1) transformed to meet ANOVA assumptions of normality and homogeneity of variance prior to analysis.

	μ				β		
Source	d.f.	MS	F	p	MS	F	p
S	2	1.26×10^{-2}	16.1	$<0.00001^{*}$	4.63	1.99	0.166
T	2	4.25×10^{-3}	5.40	0.015^{*}	72.68	31.22	$<0.0001^{*}$
S × T	4	2.55×10^{-4}	0.323	0.858	9.20	3.95	0.018^{*}
Error	18	7.87×10^{-4}			2.33		

Table 4. Coefficient estimates for (19), (12)-(13), and (18) based on previously published data for *E. affinis* collected in the Seine River Estuary, France. Coefficients that are significant at the $p = 0.05$ level are indicated with *.

Parameter	Coefficient	Estimate	p
Mortality	m_0	-1.94	0.551
	m_1	1.82×10^{-1}	0.419
	m_2	-2.59×10^{-3}	0.710
	m_3	-3.45×10^{-4}	0.587
Maturation, *b*	b_0	-3.17×10^{-1}	0.542
	b_1	1.82×10^{-1}	0.082
	b_2	-9.06×10^{-2}	0.271
	b_3	-7.93×10^{-3}	0.104
Maturation, *k*	k_0	4.22	0.025^*
	k_1	-1.77×10^{-1}	0.067
	k_2	-1.18×10^{-2}	0.499
	k_3	1.16×10^{-2}	0.070
Fecundity	f_0	-1.11	0.059
	f_1	3.84×10^{-2}	0.476
	f_2	2.63×10^{-1}	$<0.0001^*$
	f_3	-4.79×10^{-3}	0.190

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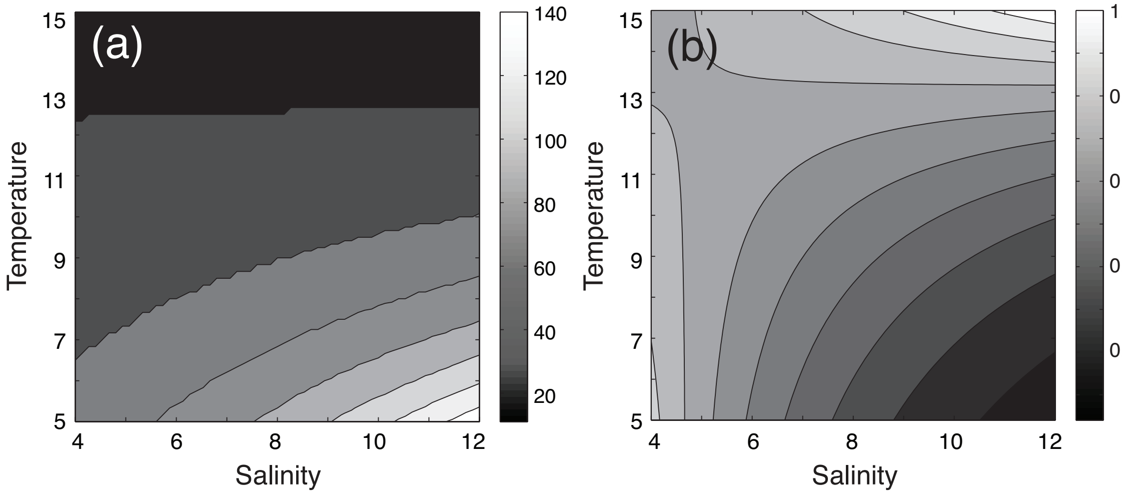

Figure 1. Parameters (a) *b* and (b) *k* as a function of temperature and salinity. The relationships are given by (a) (12) and (b) (13).

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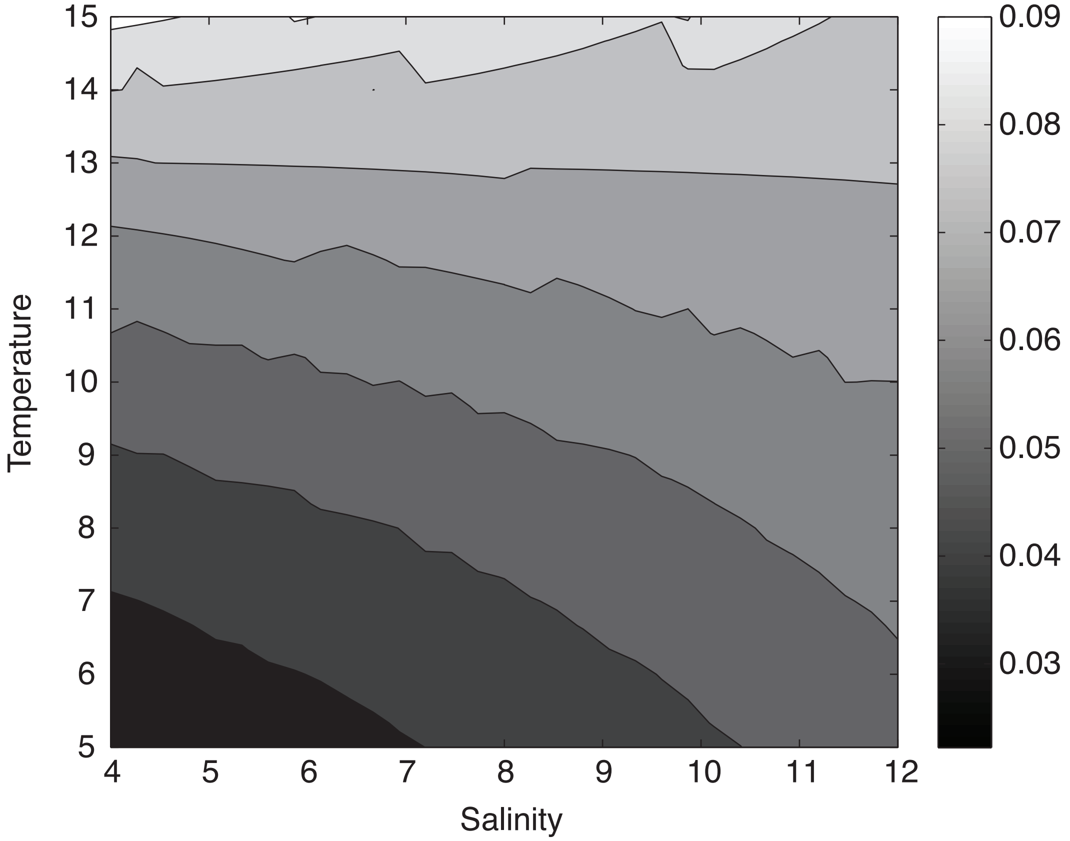

Figure 2. Maturation rate δ as a function of temperature and salinity, given by (14).

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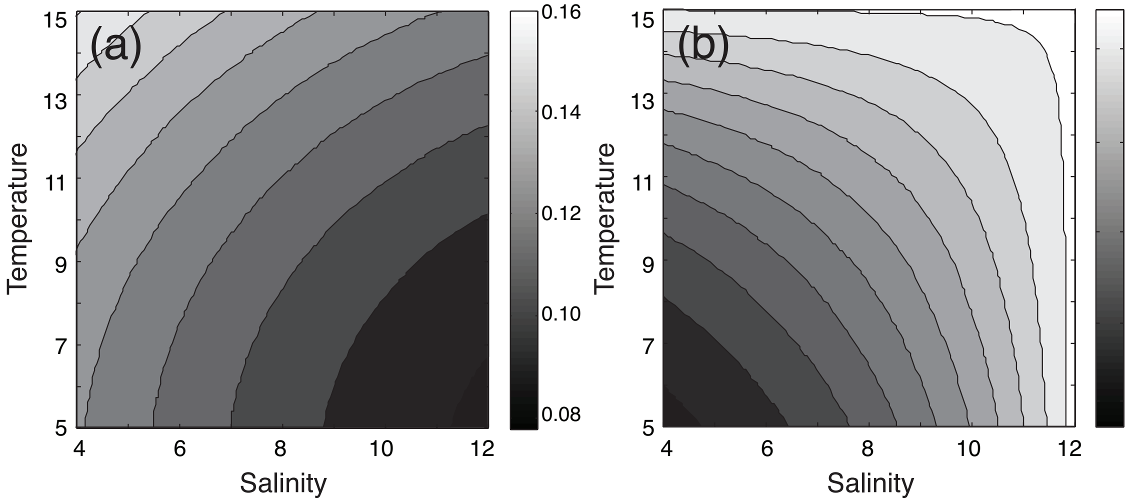

Figure 3. (a) Mortality rate, μ, as a function of temperature and salinity according to (16). (b) Fecundity, β, as a function of temperature and salinity according to (18).

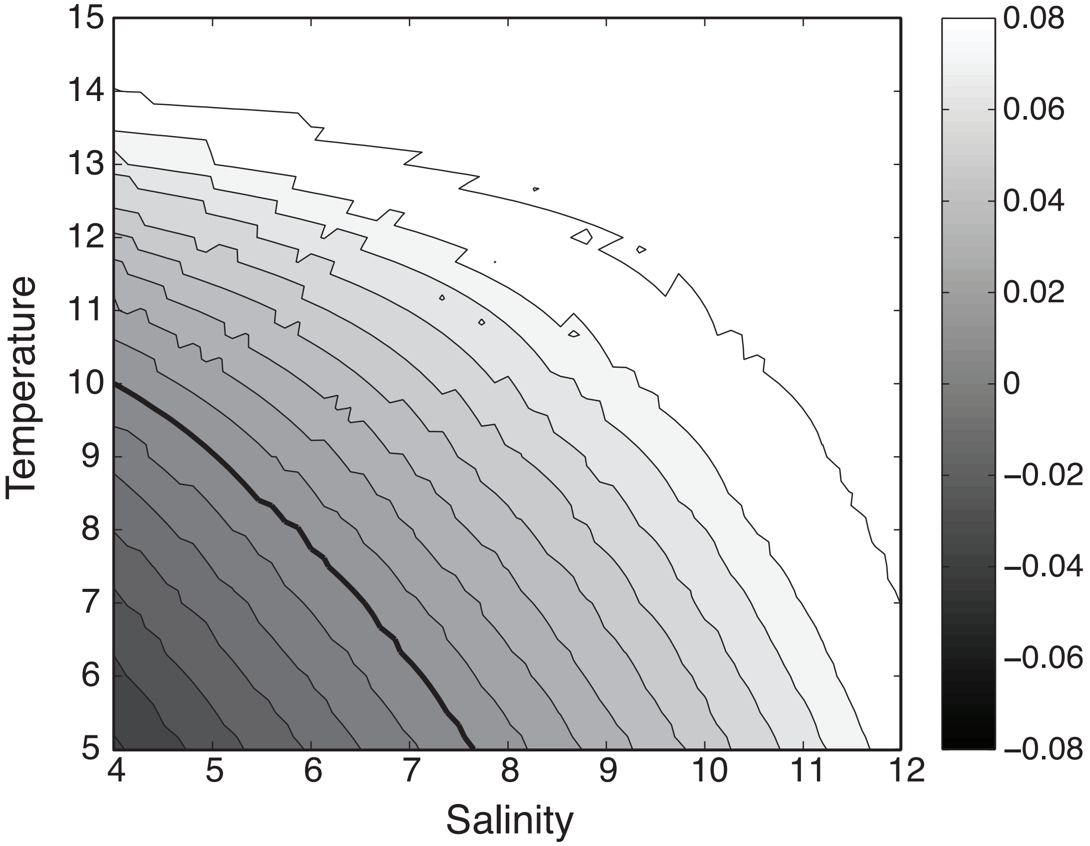

Figure 4. Population growth rate (*r*) as a function of temperature and salinity. The thicker black line corresponds to $r = 0$; above this line, $r > 0$ and the population is increasing, while and below it $r < 0$ and the population is decreasing.

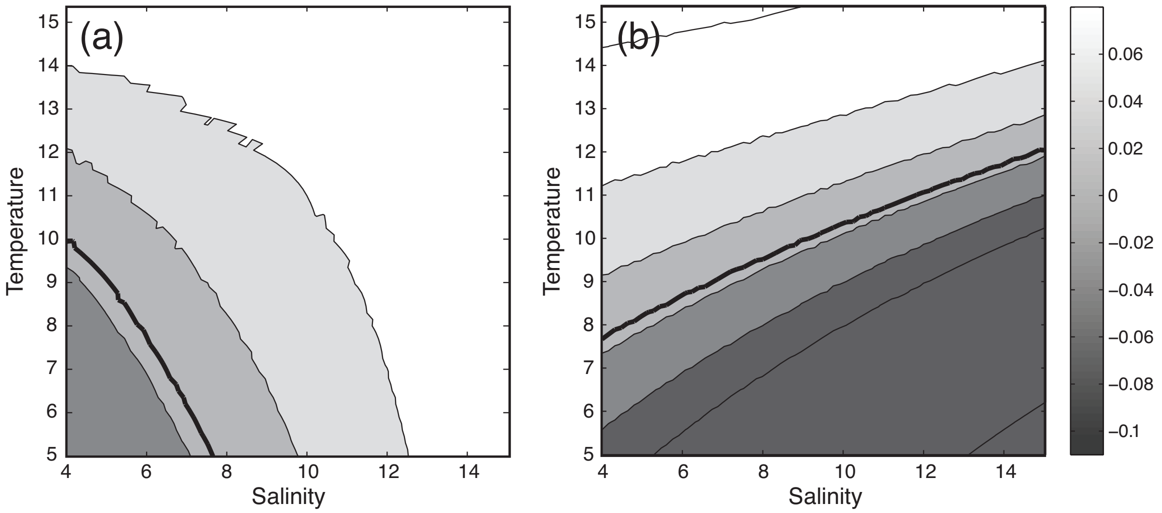

Figure 5. Population growth rate (*r*) as a function of temperature and salinity for (a) BC and (b) SE populations of *E. affinis*. The thicker black line corresponds to $r = 0$.

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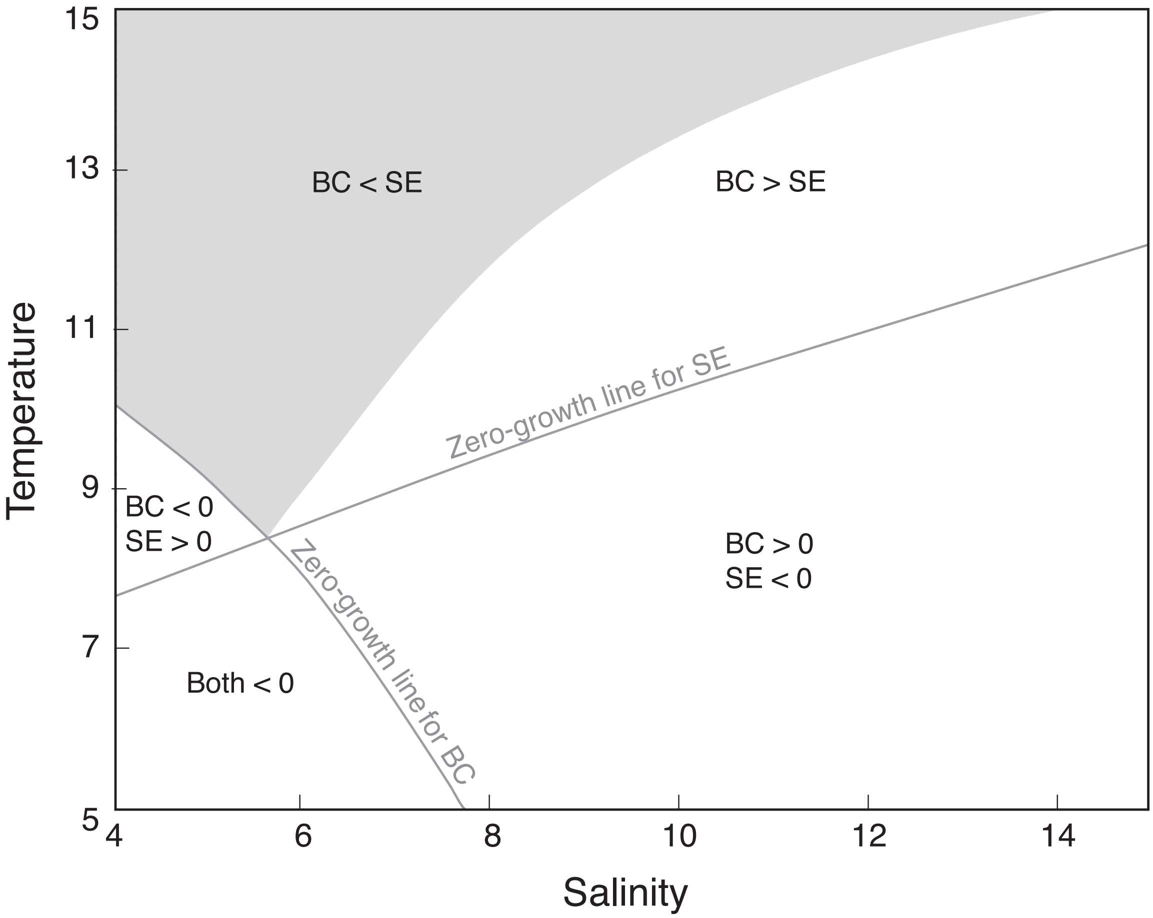

Figure 6. Relative population growth rates for BC and SE populations as a function of temperature and salinity. When growth rates are > 0, the population is growing, and when growth rates are < 0 the population is declining. Where both populations are growing, BC growth rates are higher than SE in the shaded region and lower than SE in the unshaded region.