

# Effects of variability among individuals on zooplankton population dynamics under environmental conditions

Rujia Bi<sup>1,2,\*</sup>, Hui Liu<sup>1</sup>

<sup>1</sup>Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX 77553, USA

<sup>2</sup>Present address: Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA

**ABSTRACT:** Understanding mechanisms driving biological populations in response to changes in environmental conditions could be insightful to predict ecosystem trajectories under different climate scenarios, which largely rely on modeling approaches. There is a growing consensus on variability among individuals (individual variability, IV) playing an important role in regulating dynamics and stability of populations. As a key component of marine ecosystems, changes in zooplankton dynamics could have a significant effect on ecosystem structures and fisheries production. We developed an individual-based model of a dominant coastal copepod, *Acartia tonsa*, to explore IV in sustaining a copepod population. We also examined the effects on the population dynamics under different levels of temperature, salinity, and food concentration. Abundance, egg production, and population survival of the species were used as metrics to measure population success. Our simulations suggested that the 3 environmental factors significantly influence the population dynamics of *A. tonsa*, and IV has implications for population regulation and resilience under unfavorable environmental conditions. Given that marine ecosystems are at risk from environmental changes, knowing the extent of IV in sustaining populations of key species could increase our ability to forecast ecosystem dynamics in a changing environment.

**KEY WORDS:** Individual variability · Environmental conditions · Natural selection · Population dynamics · Individual-based model · *Acartia tonsa*

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## INTRODUCTION

One of the central topics of population ecology is the study of variations in abundance and biomass at different spatial and temporal scales. The dynamics of marine populations are mainly governed by growth, reproduction, and mortality, which are often affected by various environmental factors, including abiotic factors such as temperature, nutrients, salinity, and currents (Andrewartha & Birch 1964, Jones et al. 2002, Holste & Peck 2006), and biotic factors such as food availability and quality, inter- and intraspecific competition, predation, and physiological tolerance (Begon et al. 1990, Stearns 1992, Roff

2002). Understanding how environmental and biological factors regulate population dynamics of key species could provide insights on food web dynamics and allow us to predict ecological shifts in a changing environment.

In the past few decades, environmental changes in marine ecosystems have occurred worldwide, including rising temperatures, decreasing pH, and frequent severe events such as high water temperature and changed freshwater inflow (IPCC 2001, 2007, Caldeira & Wickett 2003). Climate-driven environmental changes significantly impact the health and function of marine organisms, severely affect biodiversity, and eventually alter community structure and

\*Corresponding author: rbi@vt.edu

§Corrections were made after publication. For details see [www.int-res.com/articles/meps\\_oa/m565p269.pdf](http://www.int-res.com/articles/meps_oa/m565p269.pdf)  
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ecosystem functions (Riebesell et al. 2000, Hoegh-Guldberg et al. 2007). Research has revealed complex response patterns of organisms in terms of climate changes across multiple taxa (Stillman & Somero 2000, Ries et al. 2009). Individuals of a population often display diverse responses to environmental conditions (Båmstedt 1988, Marras et al. 2010, Fodrie et al. 2015), which may be reflected in growth, development, mortality, and reproduction, and in turn affect population structure and sustainability (Clark 2003).

Individuals are the building blocks of ecological systems, and variability among individuals (individual variability, IV) is the basis of natural selection theory (Grimm & Railsback 2013). Under increasing environmental stress, individuals that are more adaptive to the environment presumably can achieve higher fitness and have greater probability of passing genes on to subsequent generations. Rapid growth allows individuals to quickly pass the vulnerable period of high mortality at the early life stages, resulting in increased survival, younger age at maturity, and increased egg production during their lifetime (Roff 2002). For pelagic copepods, fast-developing individuals mature early and have a higher chance of survival, but because they mature at a smaller size, they may have a lower potential fecundity (Kjørboe & Hirst 2008). Magnitude and direction of selection on individuals vary with environmental pressure, resulting in diversified population structures (Rice et al. 1993, Nussey et al. 2007). Recent studies have shown that some populations could adapt to climate change via natural selection acting on existing variations in physiological responses among individuals, which could potentially increase population sustainability when experiencing environmental stressors (Hoffmann et al. 2003, Balanyá et al. 2006, Pistevo et al. 2011). Additionally, a greater degree of IV tends to appear in populations under unfavorable environmental conditions (Warwick & Clarke 1993, Pfister & Stevens 2002), which potentially indicates that a higher level of IV might help populations to be more resilient and resistant to environmental stressors.

The need to examine the impacts of IV on population dynamics has led to the rise of individual-based model (IBM) approaches. Traditional population models are largely built upon an assumption that all individuals in a population have identical life history parameters, and therefore these models center on aggregate parameters at population levels. Stage- or age-structured models allow the vital rates to vary among classes, but individuals within each class are still treated as identical (Leslie 1945, Caswell 2001).

Methodologically, the structured modeling approach has been extended to the IBM approach by endowing each individual with unique physiological traits (Batchelder & Miller 1989, Batchelder & Williams 1995). In IBM, the effects of environmental factors on each individual are distinct, but ultimately these effects are integrated to form observed overall dynamics in the population (Grimm & Railsback 2013). Although IBMs have been widely applied to test the mechanisms of a series of intrinsic and extrinsic factors in regulating the dynamics of biological populations (Letcher et al. 1996, Grimm 1999, Rose et al. 1999), studies on the confounding effects of IV and extrinsic factors on populations remain insufficient. A few studies using IBM have examined the effects of IV by only following a cohort (Rice et al. 1993, Benton 2012, Richmond et al. 2013), where attrition due to mortality is the only way population size can change. In these cases, the population cannot grow because no offspring are added into a simulation. Considering the importance of recruitment and its sensitivity to environmental conditions, it is necessary to include newly produced individuals in the model and broaden the study at a population level. Here, we developed an IBM to examine the role of IV in physiological traits in sustaining zooplankton populations with overlapping generations under various environmental factors, including temperature, salinity, and food concentration indexed as chlorophyll *a* (chl *a*).

The IBM followed the full life history of the cosmopolitan copepod *Acartia tonsa*, i.e. egg, 6 naupliar stages, 5 copepodite stages, and adult. We hypothesized that the population of *A. tonsa* may benefit from a relatively high level of IV under environmental stresses. *A. tonsa*, as a numerically abundant copepod species in the coastal Gulf of Mexico (GoM), is an important grazer on phytoplankton and a prey item for larval fish (Ortner et al. 1989, Checkley et al. 1992, Elliott et al. 2012). Therefore, the findings of our study will be insightful to better understand marine food web dynamics and fisheries production and forecast the effects of environmental changes on pelagic communities in the ocean.

## METHODS

### Model species and the physical environment

*Acartia tonsa* is distributed worldwide in nearshore marine environments, such as bays and estuaries, and can tolerate a broad range of water temperatures (−1 to 32°C) and salinity (1–38), and survive sudden

changes in environmental conditions (Mauchline 1998). The physiological processes of *A. tonsa*, such as growth, reproduction, and mortality, are highly sensitive to temperature, food availability, predation, and salinity (Berggreen et al. 1988, Purcell et al. 1994, Peck et al. 2015, Zhang et al. 2015).

Galveston Bay, the second largest estuary in the GoM and the seventh largest in the USA, supports numerous marine taxa, including fishes, shrimps, crabs, and oysters, and has been impacted by human and natural stressors for decades (Carey et al. 2013). The freshwater inflow-driven complex system in Galveston Bay (Roelke et al. 2013) provides various environmental settings to examine zooplankton dynamics in response to environmental changes.

### Description of IBM

Four biological processes (i.e. growth, development, reproduction, and mortality) were formulated in the IBM (Fig. 1). The model tracked a population of *A. tonsa* over a period of 100 d with a time step of 0.1 d. The average generation time of *A. tonsa* is 7 to 25 d (Mauchline 1998, Drillet et al. 2008, Hansen et al. 2010); thus, a period of 100 d ensured that multiple generations could be realized to allow incorporation of recruitment in the study. The model was simulated 100 times under each combination of environmental conditions. Growth was divided into growth in body carbon and growth in molt carbon. Copepod growth rate is mainly dependent on temperature, food concentration, and body weight (Liu et al. 2013). When molt carbon exceeded a threshold value, individuals molted and developed to the next stage. Given a 13-stage life history of the species, 11 molting threshold values were set in the model (no molting threshold for eggs and adults). Once mature, all assimilated carbon except metabolic carbon was set to body carbon, which was further broken down into tissue and gonads, and molt carbon was set to 0. Daily egg production rate (eggs female<sup>-1</sup> d<sup>-1</sup>) was computed from net gained gonad carbon, which was estimated as a proportion of the growth of body carbon. Mortality was assumed to be weight-dependent (Peterson & Wroblewski 1984, McGurk 1986). In the model, all individuals started from the first naupliar stage (N1). In the IBM, we adapted relevant functions from the literature, including growth and development (van Den Bosch & Gabriel 1994, Richmond et al. 2013), reproduction (Wang et al. 2014), mortality (Fager 1973,

Peterson & Wroblewski 1984, Ohman et al. 2002), and hatching success (Holste & Peck 2006). Parameter values used in the IBM are summarized in Table 1.

### Growth and development

Growth at stage  $i$  was allocated to 2 pools: body carbon ( $W_i$ ,  $\mu\text{gC}$ ) and molt carbon ( $S_i$ ,  $\mu\text{gC}$ ). Daily growth of body carbon ( $\Delta W_i$ ,  $\mu\text{gC d}^{-1}$ ) and molt carbon ( $\Delta S_i$ ,  $\mu\text{gC d}^{-1}$ ) came from the changes in assimilated carbon and metabolic carbon. Metabolic losses were assumed to be proportional to the body and molt carbon pools, respectively (Richmond et al. 2013):

$$\Delta W_i = (k \times A) - \beta_1 \times W_i \quad (1)$$

$$\Delta S_i = [(1 - k) \times A] - \beta_2 \times S_i \quad (2)$$

where  $k$  is the fraction of assimilated carbon that goes to body carbon,  $A$  is assimilated carbon ( $\mu\text{gC d}^{-1}$ ), and  $\beta_1$  and  $\beta_2$  are metabolic costs ( $\text{d}^{-1}$ ).

Assimilated carbon ( $A$ ,  $\mu\text{gC d}^{-1}$ ) is a function of food concentration and body weight (Richmond et al. 2013):

$$A = I_{\max} \times \frac{\alpha P}{1 + \alpha P} \times W_i^\theta \times \gamma \quad (3)$$

where  $I_{\max}$  is the maximum ingestion rate ( $\mu\text{gC} [\mu\text{gC copepod}]^{-1} \text{d}^{-1}$ ),  $\alpha$  is a shape parameter of the functional response relationship ( $\mu\text{gC}^{-1}$ ),  $\theta$  is a shape parameter for the effect of body weight on maximum ingestion,  $P$  is the food concentration ( $\mu\text{gC l}^{-1}$ ), and  $\gamma$  is the assimilation efficiency.

The IBM allows an individual to develop to the next stage when its molt carbon ( $S_i$ ,  $\mu\text{gC}$ ) exceeds a threshold value ( $ST_i$ ,  $\mu\text{gC}$ , values in Table 2). After molting, molt carbon was reset to 0. The processes of feeding, assimilation, buildup of carbon for the next molt, and molting were repeated until the individual reached the adult stage.

### Reproduction

The eggs produced by adult females determine the initial population abundance of the next generation. When a female individual grows to the adult stage, all assimilated carbon in excess of metabolism is devoted to body carbon ( $W$ ,  $\mu\text{gC}$ ), which is divided into 2 parts: tissue carbon ( $W_S$ ,  $\mu\text{gC}$ ) for somatic growth, and gonad carbon ( $W_E$ ,  $\mu\text{gC}$ ) for reproduction (Hirst & McKinnon 2001). The proportion of mass accumulation in gonad carbon to body carbon ( $f_E$ )

was modeled as a function of body carbon (Wang et al. 2014):

$$f_E \begin{cases} 0 & (W < W_{\min}) \\ \frac{W - W_{\min}}{W_{\max} - W_{\min}} & (W_{\min} \leq W \leq W_{\max}) \\ 1 & (W > W_{\max}) \end{cases} \quad (4)$$

where  $W$  is body carbon weight,  $W_{\min}$  is the minimum body weight for a female to start reproduction, and  $W_{\max}$  is the maximum body weight for a female to devote all assimilated energy to egg production.

Daily egg production rate of a single female was computed using net gained gonad carbon divided by the average weight of an egg, then multiplied by a temperature-dependent transformation efficiency between gonad weight and eggs ( $E_{ep}$ , in Table 1). We used a mean value of  $0.035 \mu\text{gC egg}^{-1}$  (Ambler 1985). Eggs produced within 1 d were taken as 1 clutch, and an individual female may produce a maximum of 20 clutches during her lifetime (Mauchline 1998).

To better realize population dynamics, newly produced eggs were added to the population after hatching. Hatching success ( $HS$ , %) was a function of temperature ( $T$ ) and salinity ( $S$ ). The effects of temperature and salinity are confounding; here, we formulated the effects of temperature and salinity as reported by Holste & Peck (2006):

$$HS = (3.8 \times T + 5.73) \times \left[ \left( \frac{62.74}{1 + e^{-0.44 \times (S - 6.63)}} \right) + 15.15 \right] / 100 \quad (5)$$

Newly produced eggs needed a short period to hatch before recruiting to the population. Hatching time ( $HT$ , h) was considered a function of water temperature (Holste & Peck 2006):

$$HT = (-1.84 \times T) + 64.34 \quad (6)$$

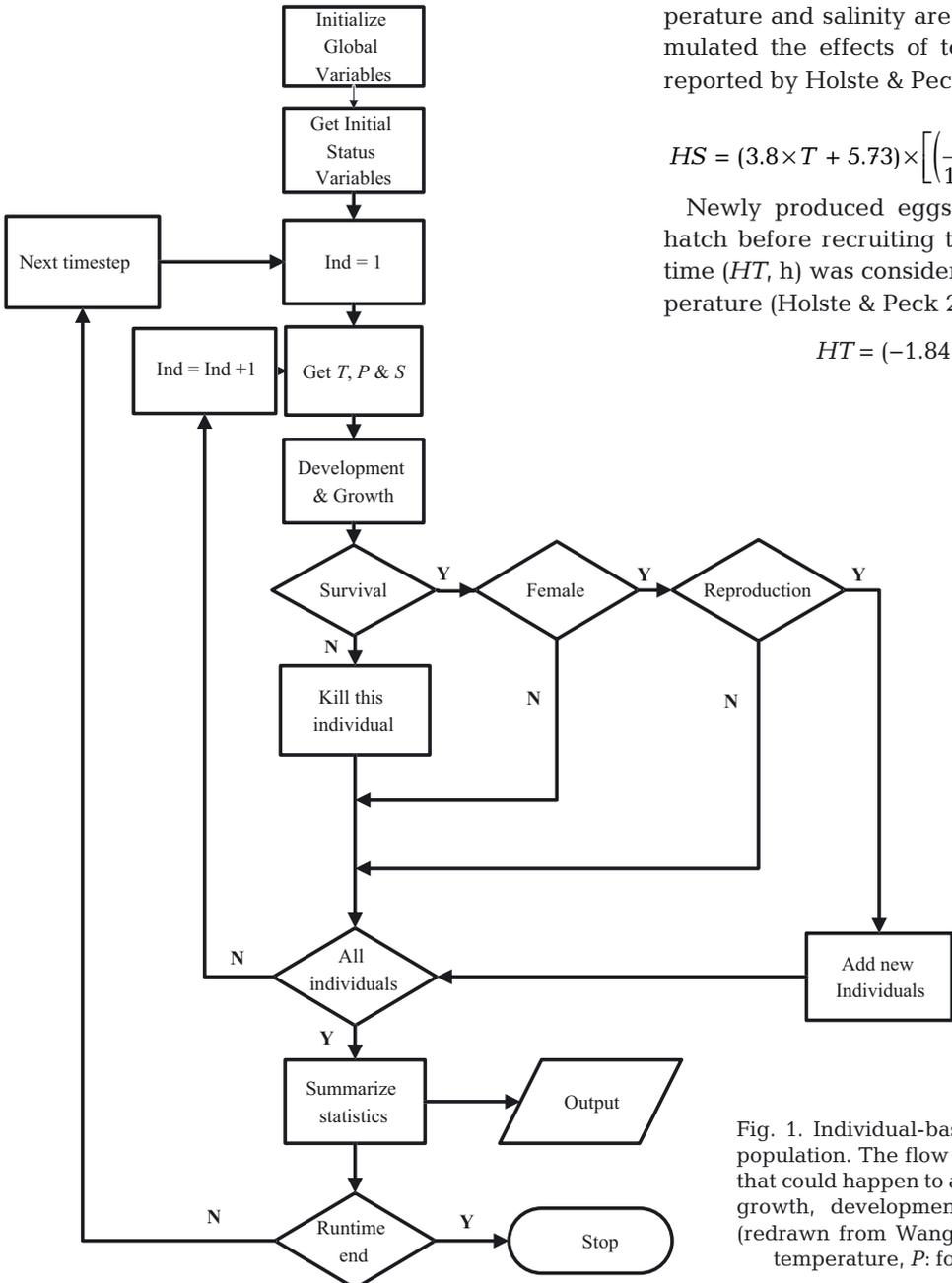


Fig. 1. Individual-based model of an *Acartia tonsa* population. The flow chart shows each of the events that could happen to an individual during its lifetime: growth, development, reproduction, and survival (redrawn from Wang et al. 2014). Y: yes, N: no,  $T$ : temperature,  $P$ : food concentration,  $S$ : salinity

Table 1. Parameters used in the individual-based model of *Acartia tonsa* population dynamics

Variable	Description	Units	Value	Source
$I_{\max}$	Maximum ingestion rate	$\mu\text{gC} (\mu\text{gC copepod})^{-1} \text{d}^{-1}$	1.209	Richmond et al. (2013)
$\alpha$	Shape parameter of the functional response	$\mu\text{gC}^{-1}$	0.00675	
$\theta$	Shape parameter for the effect of body weight on maximum ingestion		0.850	
$\gamma$	Assimilation efficiency		0.504	
$\beta_1$	Metabolic costs as a proportion of body carbon	$\text{d}^{-1}$	0.132	
$\beta_2$	Metabolic costs as a proportion of molt carbon	$\text{d}^{-1}$	0.132	
$k$	Fraction of assimilated carbon accumulated as body carbon		0.866	
$W_{\min}$	Minimum body weight for a female to start reproducing	$\mu\text{gC}$	3.24	Durbin et al. (1983)
$W_{\max}$	Maximum body weight for a female to devote all assimilated energy to egg production	$\mu\text{gC}$	7.30	
$E_{\text{ep}}$	Transformation efficiency between gonad weight and eggs	$\begin{cases} \min(-0.2408 + 0.0267 \times T^2, 1.0) \\ (T \leq 24) \\ \max(0.4 - 0.0488 \times (T - 24), 0) \\ (T > 24) \end{cases}$	Holste & Peck (2006)	
<sup>a</sup> T is temperature ( $^{\circ}\text{C}$ )				

Table 2. *Acartia tonsa* molt carbon in each stage. N: naupliar, C: copepodite. Source: Richmond et al. (2013)

Stage	Molt carbon threshold ( $\mu\text{gC}$ )
N1	0.0138
N2	0.0191
N3	0.0267
N4	0.0372
N5	0.0522
N6	0.0722
C1	0.1007
C2	0.1417
C3	0.1933
C4	0.2719
C5	0.3660

### Mortality

Stage-specific mortality rate is a major factor governing copepod population dynamics, and is subjected to temperature, food, predation, and population density (Ohman & Hirche 2001). Predation on average accounts for up to 60 to 75% of total mortality (Hirst & Kiørboe 2002). Another form of mortality to be considered is cannibalism due to feeding by adults and late copepodite stages on eggs (Roman 1977, Lemus 2006). A density-dependent cannibalism effect of C4s, C5s, and adults on eggs was incorporated in the IBM using a linear function of the integrated abundance of C4s, C5s, and adults (Ohman et al. 2002, Maps et al. 2010, 2011, Wang et al. 2014):

$$M_{\text{egg}} = 8 \times 10^{-3} \times Abun \quad (7)$$

where  $M_{\text{egg}}$  is egg mortality ( $\text{d}^{-1}$ ), and  $Abun$  is the integrated abundance of C4s, C5s, and adults.

Previous studies showed that mortality increases with temperature in both broadcast and sac-spawning copepods (Hirst & Kiørboe 2002). Therefore, we adjusted egg mortality using  $Q_{10}^{(T-T_{\text{ref}})/10}$ , where  $Q_{10} = 1.3$  is the increase in rate caused by a  $10^{\circ}\text{C}$  increase in temperature (Schmidt-Nielsen 1997) and  $T_{\text{ref}} = 15^{\circ}\text{C}$  is a reference temperature. While egg mortality is density dependent at high population abundance, it is independent of population density when adults are at low abundance (Ohman et al. 2002). Consequently, in the IBM, egg mortality was reset to 0.5 when it was lower than 0.5 due to low abundance of C4s, C5s, and adults (Wang 2012). At each time step, the number of surviving eggs was reduced exponentially (Eq. 8; Fager 1973). After a hatching period, eggs surviving to N1s were added to the simulated population:

$$N_{t+\Delta t} = N_t \times e^{-M_{\text{egg}} \times \Delta t} \quad (8)$$

where  $M_{\text{egg}}$  is egg mortality ( $\text{d}^{-1}$ ),  $t$  is the present time,  $\Delta t$  is the time step,  $N_t$  is egg abundance at present, and  $N_{t+\Delta t}$  is egg abundance after a time step.

Stage-specific mortality varies ontogenetically. Different mortality patterns have been observed in copepod populations. Some researchers have proposed that small-bodied individuals in early stages might minimize visual predation, which might benefit the population by reducing potential predation (Liu &

Hopcroft 2008). Others found a more complex pattern, with mortality rates being highest for eggs, lower for early nauplii stages, lower still for late nauplii stages, lowest for early copepodite stages, and high again for late copepodite stages (Bi et al. 2011). Among multiple patterns, decreasing mortality rates of marine pelagic organisms with increasing body size is widely accepted (Peterson & Wroblewski 1984). Therefore, weight-dependent mortality was adapted for naupliar (N1 to N6), copepodite (C1 to C5), and adult stages (Eq. 9). In our model, with the exception of the egg stage, mortality ( $M$ ) was formulated to decrease with increasing dry body weight ( $W_{\text{dry}}$ , g) (Peterson & Wroblewski 1984):

$$M = 5.26 \times 10^{-3} \times W_{\text{dry}}^{-0.25} \quad (9)$$

The dry weight of individuals was calculated by assuming that the carbon content was 40% of dry weight (Omori & Ikeda 1984). Although the mortality scaled as the  $-0.25$ th power of dry weight was derived from data of juvenile and adult fish (Peterson & Wroblewski 1984), it was subsequently shown to fit the mortality and dry weight for other marine organisms (McGurk 1986, 1987). The mortality rates of naupliar, copepodite, and adult stages were also adjusted by using the  $Q_{10}$  term. Survival or death of each individual was evaluated at each time step. A uniform random number between 0 and 1 was generated, and if the random number was less than its probability of mortality, the individual died and was removed from the simulation (Batchelder & Williams 1995, Batchelder et al. 2002).

### Initial condition and IV

Each simulation began with 100 individuals of N1 with initial molt carbon ( $S_0$ ) set to 0. Initial body carbon ( $W_0$ ) was set using a normal distribution with mean ( $\mu$ ) = 0.2  $\mu\text{gC}$ , standard deviation (SD) = 10%  $\times \mu$ , and minimum and maximum values were set as  $\mu \pm 2\text{SD}$  (Richmond et al. 2013).

We assigned the 4 physiological parameters  $I_{\text{max}}$ ,  $\alpha$ ,  $\beta_1$ , and  $\beta_2$  to each individual, and assumed them to be normally distributed. Mean values were adapted from Richmond et al. (2013). IV was defined as a coefficient of variation (CV). SD was calculated based on mean values and predefined IV (SD = mean  $\times$  IV). The 4 parameters were assigned to individuals in a related format:  $I_{\text{max}}$  was positively correlated with  $\alpha$ , and negatively correlated with  $\beta_1$  and  $\beta_2$  (Richmond et al. 2013). Therefore, an individual with higher  $I_{\text{max}}$  and  $\alpha$ , but lower  $\beta_1$  and  $\beta_2$ , is considered

an efficient feeder and fast grower. For each simulation, each individual was assigned a coefficient following a standard truncated normal distribution ( $\mu = 0$ , SD = 1, maximum and minimum values =  $\mu \pm 2\text{SD}$ , Richmond et al. 2013). Each physiological parameter of an individual was computed as the coefficient times the SD of the parameter plus the corresponding mean value (Richmond et al. 2013). We used the same coefficient for  $I_{\text{max}}$  and  $\alpha$ , but the negative value of the coefficient for  $\beta_1$  and  $\beta_2$  to set a positive correlation between  $I_{\text{max}}$  and  $\alpha$  and a negative correlation between  $I_{\text{max}}$  and  $\beta_1$  and  $\beta_2$  (Richmond et al. 2013). In this way, each parameter followed a normal distribution, but all 4 parameters were completely correlated.  $I_{\text{max}}$ ,  $\alpha$ ,  $\beta_1$ , and  $\beta_2$  were adjusted with  $Q_{10}^{(T-T_{\text{ref}})/10}$  for all temperature levels (Richmond et al. 2013). All parameter values were assumed to be appropriate for  $T_{\text{ref}} = 18^\circ\text{C}$ , a typical water temperature of Galveston Bay in spring (Liu et al. in press). We adjusted the 4 parameters assuming a  $Q_{10}$  value of 2.0, which is commonly used for copepods (Kjørboe et al. 1982, Durbin & Durbin 1992, Richmond et al. 2013).

### Simulation experiments

A factorial experimental design was applied to test the effects of IV on abundance (no. of individuals), egg production (no. of eggs), and population survival (unitless) under different environmental conditions. Four factors including temperature, food concentration, salinity, and IV were combined in the simulation experiments.

The annual seawater temperature in Galveston Bay ranged from 12 to 32°C from 2006 to 2012 (NOAA Buoy Stations GTOT2 and GNJT2). The bay showed moderate or low phytoplankton biomass, with typical values of 13 to 17  $\mu\text{g chl } a \text{ l}^{-1}$  in the upper bay (Strong 1977, Krejci 1979, Smith 1983) and 3.8 to 14.6  $\mu\text{g chl } a \text{ l}^{-1}$  in the middle to lower bay (Santschi 1995). Chl  $a$  was converted into carbon content to represent food concentration in the model with the commonly used C:chl ratio of 40 (Gamier et al. 1989). Salinity affected by freshwater inflow showed large spatial and temporal variations, ranging from 0 to 35 (Orlando 1993). We extended the ranges of the environmental factors to represent a year-round pattern likely encountered by *A. tonsa* in Galveston Bay. As a result, 6 temperature levels (12, 16, 20, 24, 28, 32°C), 8 food concentration levels (100, 200, 300, 400, 500, 600, 700, 800  $\mu\text{gC l}^{-1}$ ), and 8 salinity levels (0, 5, 10, 15, 20, 25, 30, 35) were included in the simulation

experiments. Some combinations of the 3 environmental factors could be considered typical conditions of Galveston Bay when *A. tonsa* is present. The optimal temperature for egg production of *A. tonsa* was reported between 22.9 and 24.8°C (Holste & Peck 2006), so 24°C was considered the most favorable temperature in this study. The highest food concentration level (800  $\mu\text{gC l}^{-1}$ ) was taken as the most favorable food condition. Given that hatching success of *A. tonsa* was positively correlated to salinity for a Baltic population (Holste & Peck 2006), salinity of 35 was selected as the most favorable value in this study. We should note that recent modeling work excluded the impact of salinity on a copepod population (Richmond et al. 2013) because recruitment was not considered in their models.

A common degree of variability in bioenergetic traits such as ingestion and metabolic rates in natural copepod populations is 20 to 30% (Båmstedt 1988, Richmond et al. 2013). We selected 6 levels of IV (0, 10, 20, 30, 40, 50%) in this study. Overall, there were  $6 \times 8 \times 8 \times 6$  treatment combinations of the 4 factors. The effects of IV on population dynamics of *A. tonsa* under individual environmental factors were tested in 2-factor factorial experiments (Expts 1, 2, and 3 in Table 3). Specifically, Expt 1 examined effects of IV on abundance, egg production, and population survival under different temperatures, with favorable salinity and food concentration. Expt 2 examined effects of IV on abundance, egg production, and population survival under different food concentrations, with favorable temperature and salinity. Expt 3 examined effects of IV on abundance, egg production, and population survival under different salinities, with favorable temperature and food concentration. Additionally, the multiple factorial experiment (Expt 4 in Table 3) allowed us to test the relative importance of each of the 4 factors on regulating population survival of *A. tonsa*.

### Analytical methods

For each 2-factor factorial experiment (Expts 1, 2, and 3), 2-way analysis of variance (ANOVA) was conducted to test the effects of the corresponding environmental factors and IV on population abundance and egg production. A generalized additive model (GAM) was applied to test the comprehensive effects of environmental factors and IV on population survival represented by survival ratios in 100 simulations, i.e. the number of simulations with a final abundance >0 divided by 100. GAM is advantageous

Table 3. Design of simulation experiments. *T*: temperature (°C), *P*: food concentration ( $\mu\text{gC l}^{-1}$ ), *S*: salinity, *IV*: variability among individuals (%), +/-: presence/absence in the experiment

Factor	Experiment				Factor	Experiment					
	1	2	3	4		1	2	3	4		
<i>T</i>	12	+	-	-	+	<i>IV</i>	0	+	+	+	+
	16	+	-	-	+		10	+	+	+	+
	20	+	-	-	+		20	+	+	+	+
	24	+	+	+	+		30	+	+	+	+
	28	+	-	-	+		40	+	+	+	+
	32	+	-	-	+		50	+	+	+	+
<i>P</i>	100	-	+	-	+	<i>S</i>	0	-	-	+	+
	200	-	+	-	+		5	-	-	+	+
	300	-	+	-	+		10	-	-	+	+
	400	-	+	-	+		15	-	-	+	+
	500	-	+	-	+		20	-	-	+	+
	600	-	+	-	+		25	-	-	+	+
	700	-	+	-	+		30	-	-	+	+
	800	+	+	+	+		35	+	+	+	+

when the relationship between response variable and predictor variables is nonlinear (Hastie & Tibshirani 1990). GAM can examine the effect of each predictor variable ( $x$ ) on the response variable ( $y$ ), present the effect of  $x$  on  $y$  using a smooth curve indicated as  $s(x)$ , and estimate the degrees of freedom (df) for each smoother. Degrees of freedom represent the amount of smoothing, such that  $\text{df} = 1$  indicates a linear relationship of the predictor variable with the response variable. A  $\text{df}$  of  $n$  indicates approximately an  $n$ th effect of the predictor variable on the response variable (Wood 2006). Akaike's information criterion with a correction (AICc) for finite sample sizes was used as the criterion to select the best GAM (Burnham & Anderson 2002).

In the 4-way factorial experiments, a polynomial regression model was built to test the relative importance of temperature, food concentration, salinity, and IV on population survival by comparing standardized partial regression coefficients (Bring 1994).

## RESULTS

### Expt 1: IV and temperature

Both temperature and IV had a significant main effect ( $p < 0.01$ ), and a significant interactive effect ( $p < 0.01$ ) on abundance and egg production.

Temperature had significant influence on population abundance ( $F_{5,3564} = 34\,323.41$ ,  $p < 0.01$ , Fig. 2a) and egg production ( $F_{5,3564} = 296\,371.80$ ,  $p < 0.01$ , Fig. 2b). Abundance (Fig. 2a) and egg production

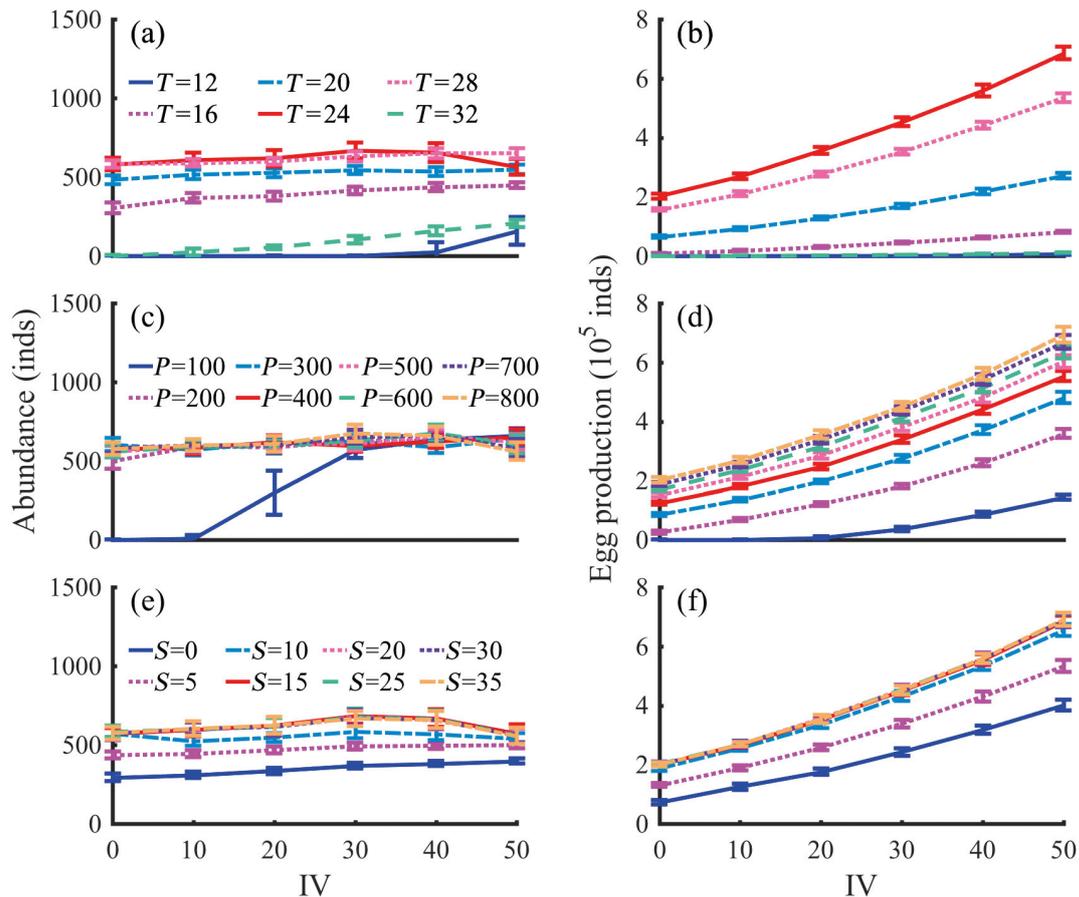


Fig. 2. (a,c,e) Mean abundance and (b,d,f) mean egg production of *Acartia tonsa* over 100 d over 100 simulations for different degrees of variability among individuals (IV, %) under different temperatures ( $T$ , °C), with favorable food concentration ( $P$ ;  $800 \mu\text{gC l}^{-1}$ ) and favorable salinity ( $S$ ; 35) (Expt 1; a,b); for different degrees of IV under different  $P$  levels, with favorable  $T$  ( $24^\circ\text{C}$ ) and favorable  $S$  (35) (Expt 2; c,d); and for different degrees of IV under different  $S$ , with favorable  $T$  ( $24^\circ\text{C}$ ) and favorable  $P$  ( $800 \mu\text{gC l}^{-1}$ ) (Expt 3; e,f). Error bars represent SE over the corresponding 100 simulations

(Fig. 2b) were higher at intermediate temperatures (24 and  $28^\circ\text{C}$ ) than at high ( $32^\circ\text{C}$ ) and low ( $12^\circ\text{C}$ ) temperatures. The effect of temperature on abundance and egg production was due to temperature-dependent growth rate, mortality, transfer efficiency between gonad weight and eggs, and hatching rate (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m546p009\\_supp.pdf](http://www.int-res.com/articles/suppl/m546p009_supp.pdf)).

IV exhibited significant effects on abundance ( $F_{5,3564} = 769.67$ ,  $p < 0.01$ , Fig. 2a), and temperature and IV had a significant interaction ( $F_{25,3564} = 121.37$ ,  $p < 0.01$ ). Population abundance increased with increasing IV except at  $24^\circ\text{C}$ , and the increases were larger at unfavorable temperature levels (12 and  $32^\circ\text{C}$ ) than at favorable settings. At  $12^\circ\text{C}$ , the mean abundance was the same (0) when IV ranged from 0 to 30%, but when IV increased from 40 to 50%, mean abundance showed a ~6-fold increase (24.96 at IV = 40% to 156.95 at IV = 50%,  $F_{1,198} = 148.11$ ,  $p < 0.01$ ).

At  $32^\circ\text{C}$ , the mean abundance increased from 0.99 at IV = 0 to 206.59 at IV = 50%, and IV had a significant effect on abundance ( $F_{5,594} = 1509.10$ ,  $p < 0.01$ ). However, at  $24^\circ\text{C}$ , not all IVs were significantly different from others ( $F_{1,198} = 2.02$ ,  $p > 0.1$  test between IV = 10 and 20%), and the mean abundance decreased 3% from IV = 0 to 50% (581.70 at IV = 0 to 564.81 at IV = 50%).

IV also showed a significant effect on egg production ( $F_{5,3564} = 48576.20$ ,  $p < 0.01$ , Fig. 2b), and the magnitude of the effect was temperature dependent, i.e. the interaction between temperature and IV was significant ( $F_{25,3564} = 8817.60$ ,  $p < 0.01$ ). Egg production also increased with increasing IV, and the relative increases were greater under unfavorable temperature. The mean egg production when IV varied from 0 to 50% was about 65 times higher at  $12^\circ\text{C}$  (93.37 at IV = 0 to 6023.30 at IV = 50%) and about 187 times higher at  $32^\circ\text{C}$  (52.00 at IV = 0 to 9677.65 at

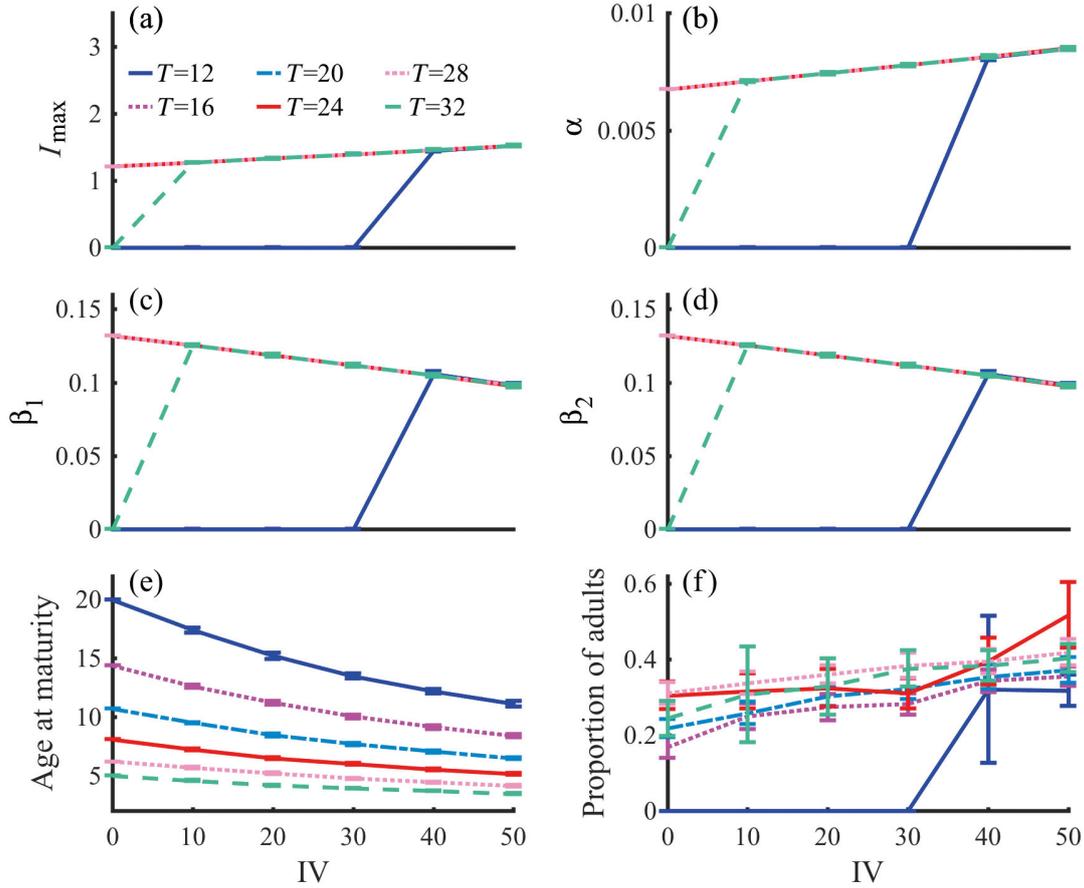


Fig. 3. Expt 1. (a–d) Mean traits of surviving *Acartia tonsa* over 100 d, (e) mean age at maturity of the original individuals, and (f) mean proportion of adults over 100 d over 100 simulations for different degrees of individual variability (IV, %) under different temperatures ( $T$ , °C). Error bars represent SE over 100 simulations. See Table 1 for the definition of the 4 traits. Values of 0 for the 4 traits imply that there were no survivors. All simulations were performed under favorable food concentration ( $800 \mu\text{gC l}^{-1}$ ) and favorable salinity (35)

IV = 50%), but only about 3 times higher at 24°C (202 536.20 at IV = 0 to 685 502.20 at IV = 50%) and 28°C (156 774.30 at IV = 0 to 534 860.70 at IV = 50%).

The effect of IV on population abundance and egg production was related to the faster-growing individuals characterized by higher ingestion rates with larger  $I_{\max}$  and larger  $\alpha$  and lower metabolism rates with smaller  $\beta_1$  and  $\beta_2$  (Fig. 3a–d). For example, at 24°C, the average  $I_{\max}$  and  $\alpha$  values of individuals surviving over the entire simulation period increased 26 and 27% from IV = 0 to 50%, respectively ( $I_{\max}$  = 1.21 at IV = 0 to 1.52 at IV = 50%, Fig. 3a;  $\alpha$  = 0.0067 at IV = 0 to 0.0085 at IV = 50%, Fig. 3b), while the average  $\beta_1$  and  $\beta_2$  values decreased 23% from IV = 0 to 50% (0.13 at IV = 0 to 0.10 at IV = 50%, Fig. 3c,d). Faster growth benefited individuals by allowing them to shorten the vulnerable early life stages and mature early (Fig. 3e), produce a larger proportion of adults (Fig. 3f), and have a higher daily egg production (Fig. 4a–f).

The best fitted GAM showed that temperature and IV both exhibited significant effects on population survival ( $p < 0.01$ ).  $s(T)$ , the effect of temperature on population survival presenting the trend of population survival as a function of temperature with constant IV, peaked around the optimal values (24 to 28°C), and tapered off at low and high values (Fig. 5a). The estimated edf (edf) of  $s(T)$  was 2.1, representing a 2.1st-degree polynomial function needed to fit the spline. IV and survival were positively correlated, because  $s(IV)$ , the trend of population survival as a function of IV with constant temperature, increased with increasing IV (Fig. 5b). The edf of  $s(IV)$  was 1.85, indicating that the relationship between IV and survival was not linear. Under unfavorable temperature, survival was low at IV = 0, and improved as IV increased (Fig. 5c). Specifically, without variability (IV = 0), to obtain 100% survival, temperature should be between 16 and 30°C. When temperature is extreme (32°C), to

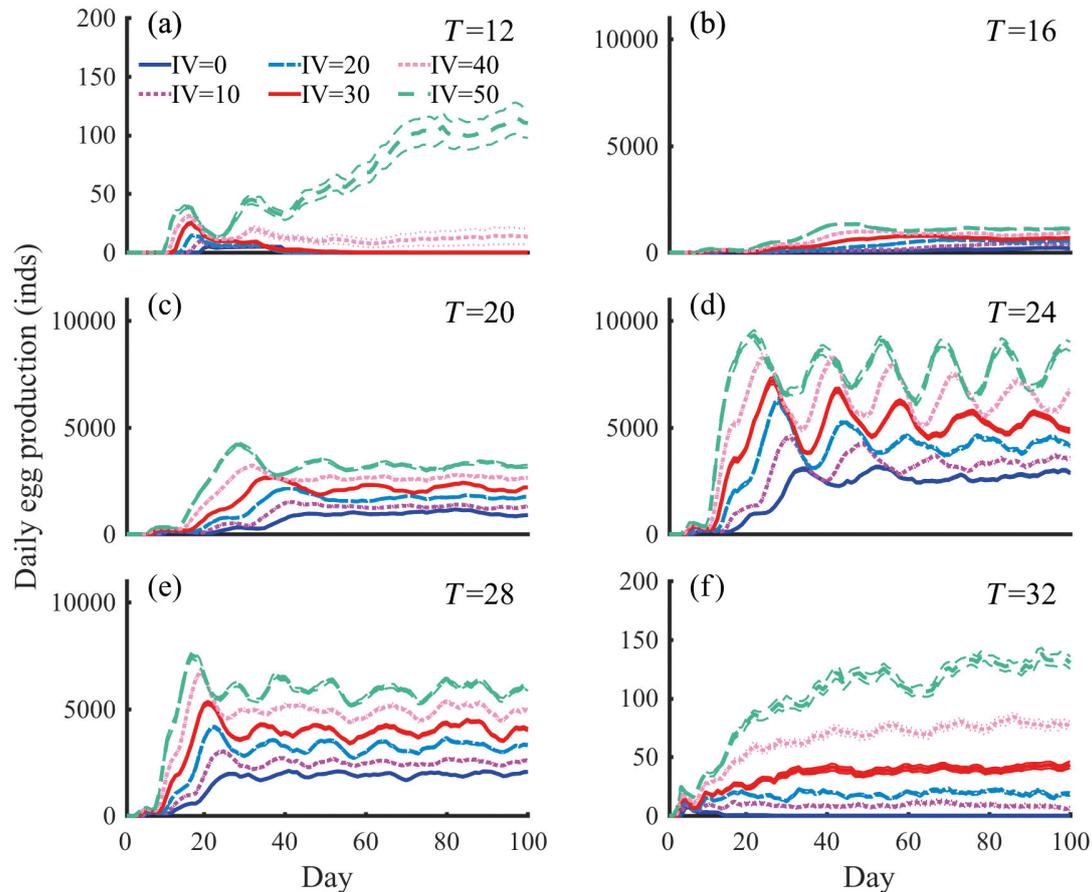


Fig. 4. Expt 1. (a–f) Mean daily egg production of *Acartia tonsa* over 100 simulations for different degrees of individual variability (IV, %) under 6 temperatures ( $T$ , °C). Thinner lines show 95 % CIs. All simulations were performed under favorable food concentration ( $800 \mu\text{gC l}^{-1}$ ) and favorable salinity (35). Note that the y-axis scales of (a) and (f) are smaller than the other plots

achieve 100 % population survival, IV should be above 29 %.

### Expt 2: IV and food concentration

Food concentration, IV, and their interaction had a significant influence on abundance and egg production ( $p < 0.01$ ). As food concentration increased, it showed less significant influence on abundance, but the effect of IV on abundance variables was still highly significant.

The impacts of food concentration were significant on population abundance ( $F_{7,4752} = 2029.50$ ,  $p < 0.01$ , Fig. 2c) and egg production ( $F_{7,4752} = 68\,203.60$ ,  $p < 0.01$ , Fig. 2d). Abundance and egg production were lower under the lowest food concentration ( $100 \mu\text{gC l}^{-1}$ ) than others, especially when IV was less than 30 %. These effects resulted from the influence of food concentration on growth rate and weight-dependent mortality (Fig. S2 in the Supplement).

IV had significant effects on abundance ( $F_{5,4752} = 1275.26$ ,  $p < 0.01$ , Fig. 2c), under low food concentration in particular ( $F_{35,4752} = 463.69$ ,  $p < 0.01$ ). For instance, at  $100 \mu\text{gC l}^{-1}$ , abundance significantly correlated with IV ( $F_{5,584} = 1893.00$ ,  $p < 0.01$ ), and the effect of each IV differed significantly from the others (i.e.  $F_{1,198} = 24.67$ ,  $p < 0.01$  test between IV = 0 and 10%;  $F_{1,198} = 29.42$ ,  $p < 0.01$  test between IV = 40 and 50 %). When IV varied from 10 to 50 %, the mean abundance increased about 46 times (14.09 at IV = 10 % to 668.69 at IV = 50 %). In contrast, at  $200 \mu\text{gC l}^{-1}$ , the mean abundance only increased 28 % from IV = 0 to 50 % (497.28 at IV = 0 to 637.66 at IV = 50 %).

IV also significantly affected egg production ( $F_{5,4752} = 120\,961.40$ ,  $p < 0.01$ , Fig. 2d), and the effects changed with food concentration ( $F_{35,4752} = 1236.20$ ,  $p < 0.01$ ). Egg production increased with increasing IV, and the increases were greater under low food conditions. The mean egg production increased as high as 37 517 times from IV = 0 to 50 % at  $100 \mu\text{gC l}^{-1}$  (3.85 at IV =

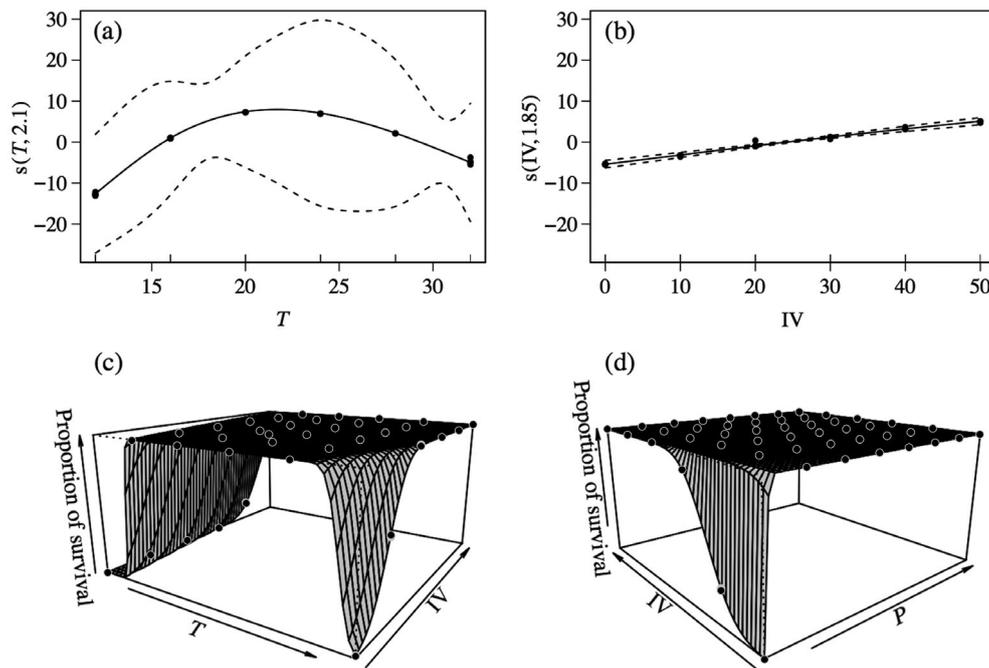


Fig. 5. Expts 1 & 2. (a,b) Expt 1: partial-regression plots of generalized additive models of *Acartia tonsa* population survival with individual variability ( $IV$ , %) and temperature ( $T$ , °C). A plot of  $x$  versus  $s(x)$  shows the relationship between  $x$  and  $y$ , holding constant the other variables in the model.  $s(T)/s(IV)$  is a smoother of the effect of temperature/ $IV$  on population survival, presenting the trend of population survival as a function of temperature/ $IV$ . Solid and dotted lines show means and 95% CIs, respectively. The number appearing in  $s(x)$  is the estimated degrees of freedom (edf), an indication of the amount of smoothing. (c) Expt 1: relationship among population survival,  $IV$ , and temperature. (d) Expt 2: relationship among population survival,  $IV$ , and food concentration ( $P$ ,  $\mu\text{gC l}^{-1}$ )

0 to 144 439.60 at  $IV = 50\%$ ), but only increased about 14 times at  $200 \mu\text{gC l}^{-1}$  (25 923.99 at  $IV = 0$  to 358 564.15 at  $IV = 50\%$ ), and even less under higher food concentrations.

Environmental selection preferred effective grazers with higher assimilation rates and lower metabolism rates (Fig. 6a–d). As  $IV$  increased, more individuals displayed greater  $I_{\max}$  and  $\alpha$ , and smaller  $\beta_1$  and  $\beta_2$ . At  $100 \mu\text{gC l}^{-1}$ , the average  $I_{\max}$  value and  $\alpha$  value of individuals surviving in the entire simulation period increased 20% from  $IV = 10$  to  $50\%$  ( $I_{\max} = 1.27$  at  $IV = 10\%$  to  $1.52$  at  $IV = 50\%$ , Fig. 6a;  $\alpha = 0.0071$  at  $IV = 0$  to  $0.0085$  at  $IV = 50\%$ , Fig. 6b); meanwhile, the average  $\beta_1$  and  $\beta_2$  values decreased 23% ( $0.13$  at  $IV = 10\%$  to  $0.10$  at  $IV = 50\%$ , Fig. 6c,d). Consequently, effective grazers had faster growth rates, leading to earlier maturation (Fig. 6e), more adults (Fig. 6f), and higher daily egg production (Fig. 7a–f).

The best selected GAM included an interactive effect between food concentration and  $IV$ , and the interaction term was significant ( $p < 0.01$ ). Except for  $100 \mu\text{gC l}^{-1}$ , populations under all other concentration levels survived completely (Fig. 5d). The

required food concentration for 100% of the population to survive when  $IV = 0$  was  $106 \mu\text{gC l}^{-1}$ . Under  $100 \mu\text{gC l}^{-1}$ ,  $IV$  should be above 34% to achieve 100% survival.

### Expt 3: $IV$ and salinity

The effects of salinity,  $IV$ , and their interaction on abundance and egg production were significant ( $p < 0.01$ ). When salinity was above 15, its effect on abundance and egg production was no longer significant, but  $IV$  still showed highly significant effects on those 2 response variables.

In addition to temperature and food concentration, population abundance ( $F_{7,4752} = 3417.92$ ,  $p < 0.01$ , Fig. 2e), and egg production ( $F_{7,4752} = 15348.65$ ,  $p < 0.01$ , Fig. 2f) of *Acartia tonsa* were significantly affected by salinity. Salinity influenced hatching rate (Fig. S3 in the Supplement), with a nonlinear relationship, such that hatching success declined markedly with decreasing salinity below a threshold of 15.

Abundance was significantly influenced by  $IV$  ( $F_{5,4752} = 545.47$ ,  $p < 0.01$ ) in different degrees under

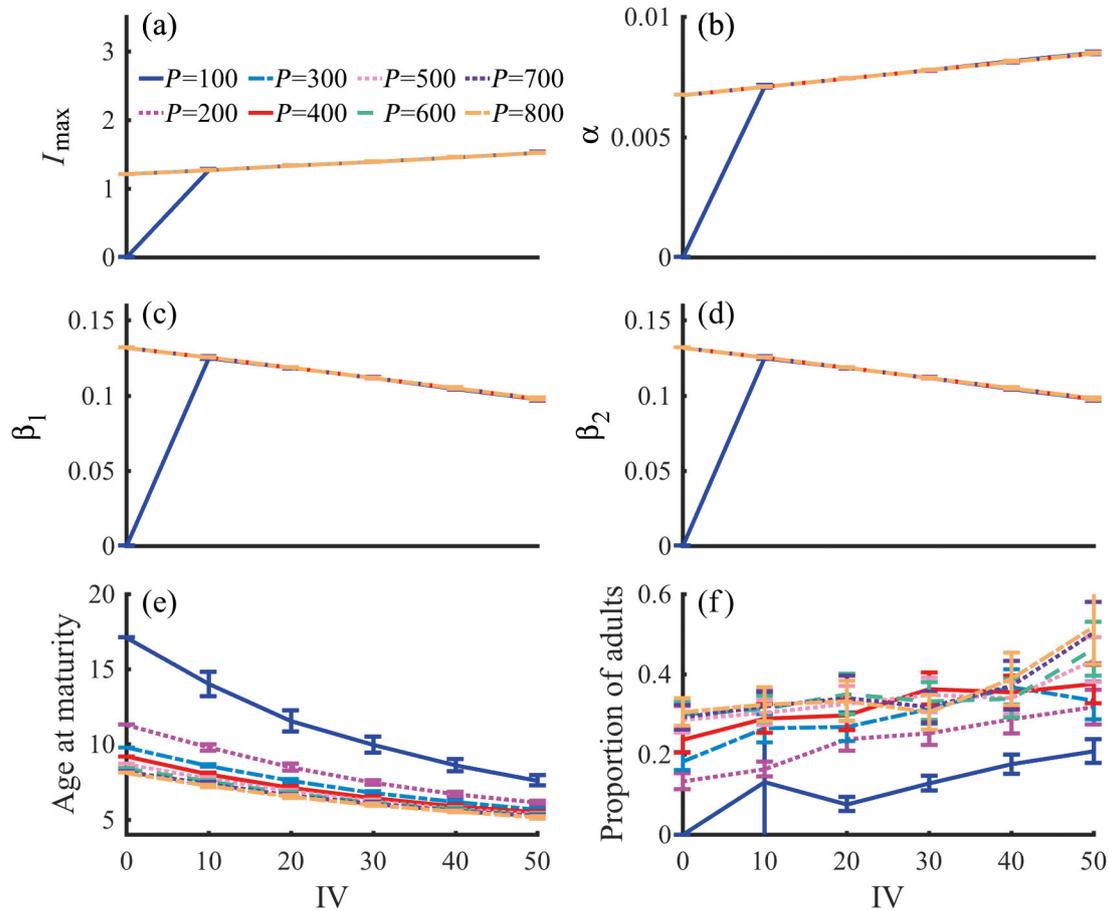


Fig. 6. Expt 2. (a–d) Mean traits of surviving *Acartia tonsa* over 100 d, (e) mean age at maturity of the original individuals, and (f) mean proportion of adults over 100 d over 100 simulations for different degrees of individual variability (IV, %) under different food concentrations ( $P$ ,  $\mu\text{gC l}^{-1}$ ). Error bars represent SE over 100 simulations. See Table 1 for definitions of the 4 traits. Values of 0 for the 4 traits imply that there were no survivors. All simulations were performed under favorable temperature (24°C) and favorable salinity (35)

different salinities ( $F_{35,4752} = 35.54$ ,  $p < 0.01$ , Fig. 2e). At low salinities, abundance increased with increasing IV. Using salinity of 0 as an extreme example, the mean abundance increased about 38% from IV = 0 to 50% (290.53 at IV = 0 to 399.54 at IV = 50%). In comparison, when salinity exceeded 15, there was no obvious increase in abundance with increasing IV ( $F_{4,2970} = 0.99$ ,  $p = 0.41$ , Fig. 2e). For example, when salinity was 20, the mean abundance decreased about 2% from IV = 0 to 50% (578.92 at IV = 0 to 569.64 at IV = 50%).

IV had significant effects on egg production ( $F_{5,4752} = 109308.81$ ,  $p < 0.01$ ). At all salinity levels, egg production increased with increasing IV, and the relative increases were greater at low salinity (Fig. 2f). In particular, when salinity was 0, mean egg production under IV = 50% was ca. 5 times greater than that under IV = 0 (73827.92 at IV = 0 to 398707.70 at IV = 50%); when salinity was 5, the mean egg produc-

tion increased about 4 times from IV = 0 to 50% (132467.60 at IV = 0 to 534971.30 at IV = 50%); when salinity was 10, the mean egg production increased ~3 times from IV = 0 to 50% (187942.50 at IV = 0 to 650855.40 at IV = 50%). As salinity increased, the increase in mean egg production from IV = 0 to 50% decreased further.

Under higher IV, there were more individuals with greater  $I_{\max}$  and  $\alpha$ , and smaller  $\beta_1$  and  $\beta_2$ . These individuals tended to be selected (Fig. 8a–d). For example, at salinity = 0, the average  $I_{\max}$  of survivors increased 26% from IV = 0 to 50% (1.21 at IV = 0 to 1.52 at IV = 50%, Fig. 8a); the average  $\alpha$  value increased 25% (0.0068 at IV = 0 to 0.0085 at IV = 50%, Fig. 8b); the average  $\beta_1$  and  $\beta_2$  values decreased 23% (0.13 at IV = 10% to 0.10 at IV = 50%, Fig. 8c,d). The selected individuals showed higher growth rates leading to earlier maturation (Fig. 8e), which resulted in a larger proportion of adults ( $F_{5,4752}$

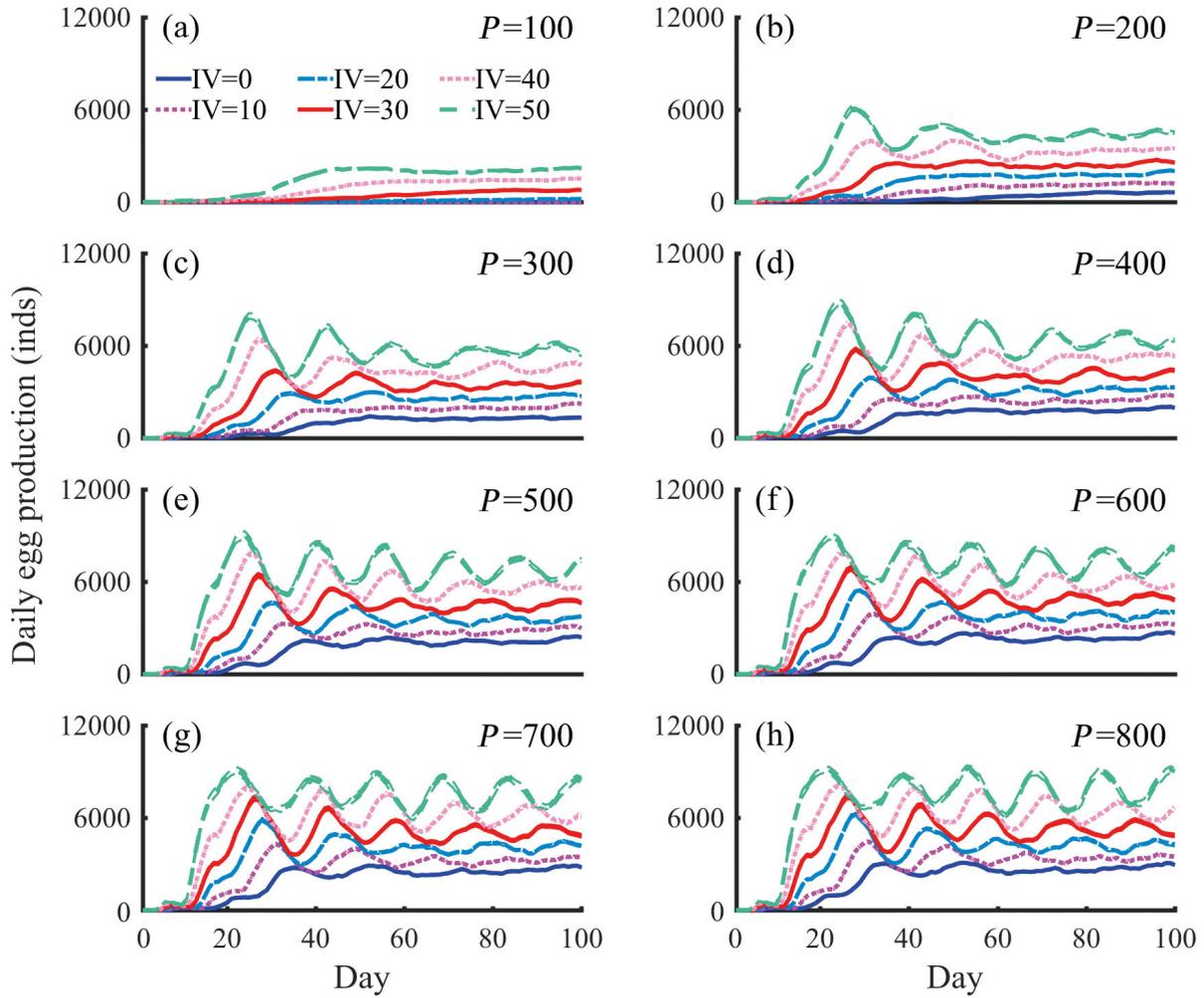


Fig. 7. Expt 2. (a–h) Mean daily egg production of *Acartia tonsa* over 100 simulations for different degrees of individual variability (IV, %) under 8 food concentrations ( $P$ ,  $\mu\text{gC l}^{-1}$ ). Thinner lines show 95% CIs. All simulations were performed under favorable temperature ( $24^\circ\text{C}$ ) and favorable salinity (35)

= 1600.90,  $p < 0.01$ , Fig. 8f) and higher daily egg production (Fig. 9a–f).

At all salinity levels, even the lowest level, populations could survive, but abundance, egg production, and proportion of adults ( $F_{7,4752} = 46.93$ ,  $p < 0.01$ , Fig. 8f) were influenced by changes in salinity.

Table 4. Standardized partial regression coefficients and p-values of independent variables in the polynomial regression model. CT: central temperature, calculated as temperature – 22 ( $^\circ\text{C}$ ),  $\text{CT}^2$ : the square of CT,  $P$ : food concentration ( $\mu\text{gC l}^{-1}$ ),  $S$ : salinity, IV: variability among individuals (%)

	CT	CT <sup>2</sup>	P	S	IV
Coefficient	2.45	-2.19	0.29	0.14	0.25
p	<0.01	<0.01	<0.01	<0.01	<0.01

#### Expt 4: Effects of temperature, food concentration, salinity, and IV on population dynamics

From Expt 1, temperature appeared to influence population abundance in a quadratic format, so the terms ‘central temperature’ (temperature minus 22) and ‘square of central temperature’ were added to replace the original temperature in a multiple regression model. All terms were highly significant (Table 4). Central temperature and the square of central temperature had greater standardized partial regression coefficients, while salinity had the lowest standardized partial regression coefficient. Given the magnitudes of standardized partial regression coefficients, temperature was the most influential factor, followed by food concentration, IV, and lastly salinity.

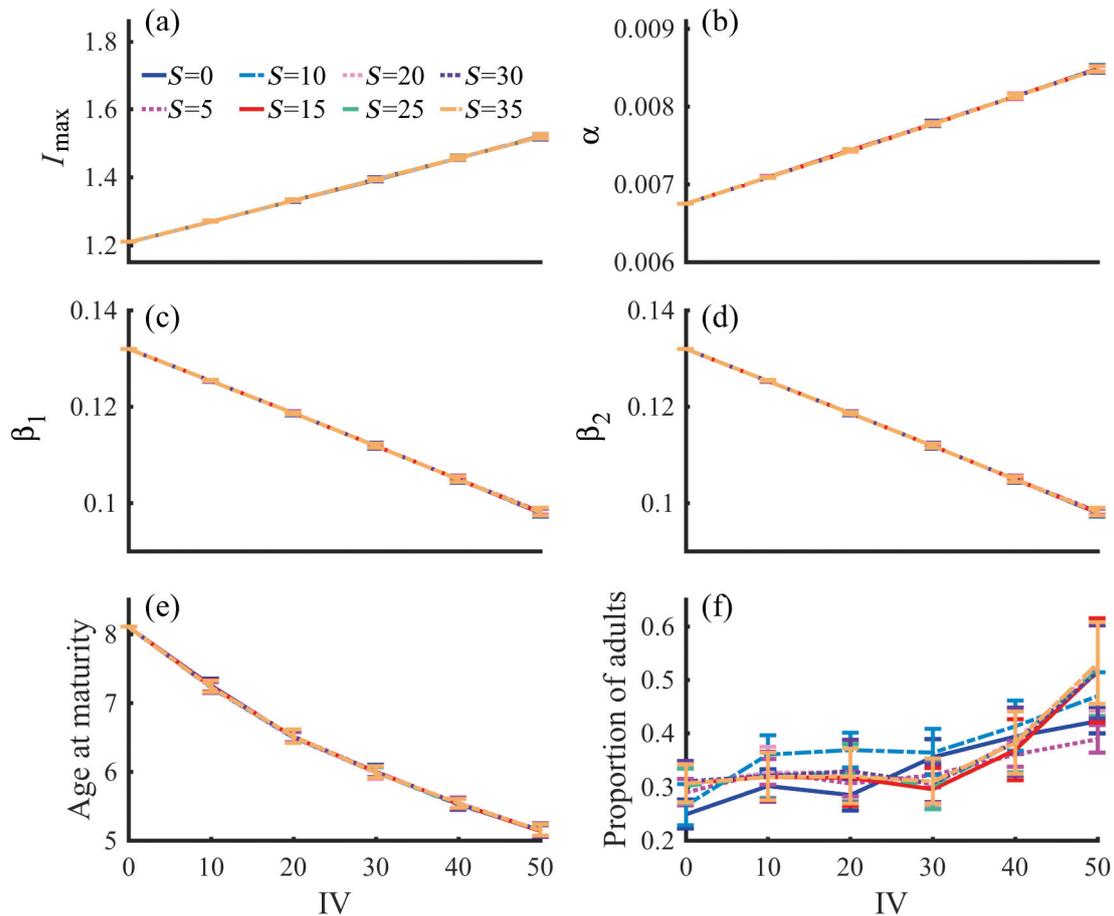


Fig. 8. Expt 3. (a–d) Mean traits of survivors of the original *Acartia tonsa* individuals over 100 d, (e) mean age at maturity of the original individuals, and (f) mean proportion of adults over 100 d over 100 simulations for different degrees of individual variability (IV, %) under different salinities (S). Error bars represent SE over the corresponding 100 simulations. See Table 1 for definitions of the 4 traits. All simulations were performed under favorable temperature (24°C) and favorable food concentration (800  $\mu\text{gC l}^{-1}$ )

## DISCUSSION

### Effects of IV

Life history traits relating to growth and reproduction often vary among species and populations as well as individuals within a population (Ergon et al. 2001). Individuals of a population may respond to the environment in their own particular ways (Walther et al. 2002, Nussey et al. 2007), which could alter population structures and trigger population responses to environmental changes (Both et al. 2004, Nussey et al. 2005a,b). Our simulations demonstrated that IV benefits populations experiencing unfavorable environmental conditions, and offers a basis for selection to operate. In the simulations, higher IV benefitted the population by increasing the proportion of more adaptive individuals and ensuring population survival under unfavorable environmental conditions.

Our simulations consistently showed that under favorable conditions, such as optimal temperature, high food concentration, and salinity, the population tended to sustain itself even without variability in the physiological traits, which is indicated by non-0 abundance in the simulations (see Fig. 2). Ideally, when environmental conditions are optimal, nearly all individuals should be able to adapt to the environment, so the role of environmental selection appears blurred, which may lessen the effects of IV on population persistence. On the other hand, although higher levels of IV can still increase population performance, the increase is not substantial and even becomes negative contingent on the environmental conditions. For example, the simulated population abundance decreased as IV increased from 40 to 50% at 24°C (see Fig. 2a). With higher IV, besides a larger portion of faster growers, a portion of individuals with smaller  $I_{max}$  and  $\alpha$ , but larger  $\beta_1$  and  $\beta_2$ , also

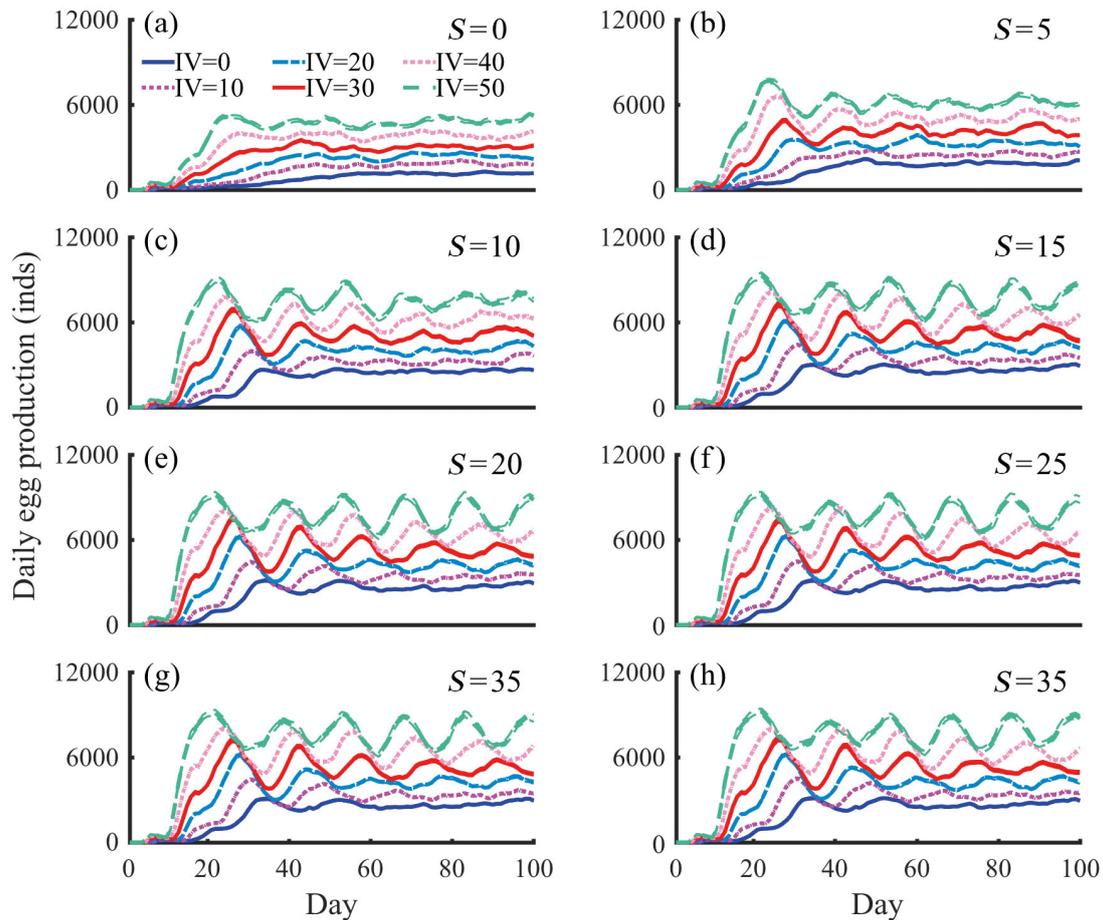


Fig. 9. Expt 3. (a–h) Mean daily egg production of *Acartia tonsa* over 100 simulations for different degrees of individual variability (IV, %) under 8 salinities ( $S$ ). Thinner lines show 95% CIs. All simulations were performed under favorable temperature ( $24^{\circ}\text{C}$ ) and favorable food concentration ( $800\ \mu\text{gC l}^{-1}$ )

appeared. These slower growers may need a longer time to mature, resulting in lower reproduction and recruitment to the population. It would be interesting to determine whether the faster growers could compensate for the increased loss of these slower growers over their life cycle. We suggest that when IV varies from 40 to 50% at  $24^{\circ}\text{C}$ , the loss from the slower growers is larger than the gain of the faster growers, resulting in the decreased abundance, which is likely due to the effects allowing slow growers to remain in the population. Under unfavorable conditions, rapid growth and earlier maturation seem more strategic to population success than slow growth with small size. The impacts of IV on morphological characteristics and life history traits have been considered an effective buffer against stressful or changing environmental conditions (Kendall & Fox 2002, Nussey et al. 2007, Schindler et al. 2010). In contrast, populations may be sustainable under optimal conditions without high levels of IV only if favorable conditions persist (King 1970).

The strength and direction of selection on individuals are influenced by environmental changes, and can generate alterations in response to the environment at population levels. In particular, the nature of environmental selection to adjust a trait of an individual becomes increasingly apparent as the magnitude of environmental stresses increases (Rice et al. 1993, Nussey et al. 2007). In our simulations, individuals with higher  $I_{\max}$  and  $\alpha$ , but lower  $\beta_1$  and  $\beta_2$ , can not only grow faster and pass the vulnerable early stages quickly, but also have higher fecundity, so they are more likely to be selected. Previous studies pointed out that pelagic copepods with faster growth might have lower fecundity (Kjørboe & Hirst 2008), so the balance of faster growth and lower fecundity needs further consideration to define adaptive individuals. At higher and unfavorable temperatures, the requirements for adaptive individuals become even more demanding, so the strength of selection tends to be evident.

Across different levels of the 3 environmental factors, under unfavorable conditions, higher levels of IV can increase population survival. In general, unfavorable conditions impose a greater challenge for a population, therefore selection on individuals with adaptive traits represented as greater  $I_{\max}$  and  $\alpha$ , but lower  $\beta_1$  and  $\beta_2$ , is stronger. These individuals presumably grow faster and mature earlier, resulting in a large proportion of adults and high daily egg production rate, which potentially increases recruitment and population abundance. The existence of more adaptive individuals with higher IV has been shown to increase population survival when populations are experiencing stressful conditions, while populations without IV die out rapidly as conditions become unfavorable (Conner & White 1999, Uchma ski 1999). Under stressful conditions, for populations with higher IV, at least some individuals tend to survive, which enables populations to resist environmental stresses and even to rebound in some cases; in contrast, when there is no IV, all individuals have moderate physiological traits, and none can survive so that the population will experience rapid collapse (Hanski 1999, Bown et al. 2007, Reed et al. 2007). Higher levels of IV in the IBM may magnify the variations in individuals responding to environmental selection, which potentially counteract the effects of selection (Holt 2003, Alleaume-Benharira et al. 2006). For a species with a short generation time and higher sensibility to environmental conditions, such as copepods, the IV could rapidly translate into meaningful effects on population dynamics, including population persistence and population density. As a key component of food web dynamics, zooplankton are tightly linked to fishes and environmental conditions (Liu et al. 2014). Therefore, the findings of impacts of IV on population dynamics of copepods have potential implications to ecosystem dynamics and fisheries production.

#### Local relevance and further points

Estuaries face increasing stresses from natural and anthropogenic sources that may cause substantial changes to the structure and function of estuarine ecosystems. Galveston Bay has been subjected to impacts of human and natural stressors for decades (Lester & Gonzalez 2003, Carey et al. 2013). At annual scales, a large variation in hydrographic conditions exists in the bay. Certain combinations of the 3 environmental factors included in our simulations likely occur seasonally at specific locations in the system. Focusing on a dominant zooplankton species in

GoM estuaries (Murrell & Lores 2004, Badylak & Phlips 2008, Liu et al. in press), the results of our IBM simulations are relevant to Galveston Bay in particular and the GoM subtropical estuaries in general.

In spring, optimal temperature and high food concentration provide favorable conditions for the *Acartia tonsa* population, resulting in a predictable abundance peak. The extreme high temperature and decreasing phytoplankton biomass during summer could cause a negative influence and hence a reduced abundance of the species. An increase in phytoplankton production in fall triggers the fall zooplankton bloom. Finally, low temperature, low food concentration, and decreasing salinity in the frigid winter stress the population and decrease abundance. At spatial scales, the high salinity in the lower bay benefits the population, which is confirmed by previous observations that the abundance of *A. tonsa* appeared to be higher in the more saline portions of estuaries closer to the GoM than in the upper fresher areas (Longley 1994, Liu et al. in press). These predictions are also consistent with field observation in GoM coastal waters. Escamilla et al. (2011) reported a significant spatial and seasonal variability of *A. tonsa* in a tropical coastal lagoon in the southern GoM. *A. tonsa* showed strong correlations with temperature and food availability, and was more abundant in the outer sector than within the inner zone, especially during the rainy season, probably avoiding lower salinity conditions in the inner zone (Escamilla et al. 2011).

During the past 50 yr, sea surface temperature in Texas bays has exhibited a gradual rise that is consistent with global warming since the 1970s (Tolan & Fisher 2009). A recent study reported evidence of climate-induced alteration of GoM ecosystems (Karnauskas et al. 2015), but details on lower trophic levels, such as zooplankton, still remain deficient. Climate-driven sea level rising and drought likely induce decreasing freshwater discharge and increasing intrusion of coastal ocean water into estuaries (Desantis et al. 2007), which potentially alter the hydrographic domain of GoM estuaries with significant ecological implications (Liu et al. in press). These changes could severely alter the direction and strength of selection on biotic populations and affect the life history of marine organisms. Especially, as the most significant environmental factor, increasing temperature in summer will harm populations, resulting in low population abundance, low survival, and even population extinction. Based on our findings, to survive in warming water, a higher level of IV under which more individuals may possess adaptive traits is needed.

Although IV ranging between 20 and 30% is considered common in natural copepod populations (Båmstedt 1988), a larger IV is expected to sustain populations under unfavorable environmental conditions (Warwick & Clarke 1993, Pfister & Stevens 2002). Our simulations, which include a wide range of IV for population regulation and stability, provide references for potential occurrences under extremely harsh conditions. In this study, IV was parameterized by allowing 4 physiological parameters ( $I_{\max}$ ,  $\alpha$ ,  $\beta_1$ , and  $\beta_2$ ) to vary among individuals in correlated normal distributions. Changes of parameterization can have an influence on the results, and future tests on the parameterization of IV and its effect on population dynamics are needed.

In conclusion, our findings show that the effects of environmental changes on population dynamics are significantly modulated by IV. Individuals can adapt to their environment to some extent, and more adaptive individuals tend to be selected. Given a changing environment increasingly subjected to natural and anthropogenic stressors, incorporating IV into modeling research on population dynamics will improve our ability to understand mechanisms of population regulation and stability in response to environmental changes and population evolution.

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