THE INFLUENCE OF INDIVIDUAL VARIABILITY ON ZOOPLANKTON POPULATION DYNAMICS UNDER DIFFERENT ENVIRONMENTAL CONDITIONS

A Thesis

by

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ABSTRACT

Understanding how biological components respond to environmental changes could be insightful to predict ecosystem trajectories under different climate scenarios. Zooplankton are key components of marine ecosystems and changes in their dynamics could have a major impact on ecosystem structures. I developed an individual-based model of a coastal calanoid copepod species *Acartia tonsa* to examine the impacts of varying environmental factors on population dynamics, and to explore the role of individual variability in sustaining a population under changing temperature, food concentration and salinity. Abundance, egg production and population survival were used to measure population success. Results suggested that *A. tonsa* benefits from a high level of individual variability under extreme environmental conditions including unfavorable temperature, salinity, as well as low food concentration, and selection for fast-growers becomes stronger with increasing environmental stress. Multiple regression analyses showed that temperature, food concentration, salinity and individual variability have significant effects on survival of *A. tonsa*. These results suggest that environmental factors have significant influence on zooplankton population dynamics, and individual variability has important implications for population resilience under unfavorable conditions. Given that marine ecosystems are at risk from drastic environmental changes, understanding how individual variability sustains populations could increase our capability to predict population dynamics in a changing environment.

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1. INTRODUCTION

One of the central topics of population ecology is to study the changes in abundance and biomass at different spatial and temporal scales. The dynamics of marine populations are 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 intra-specific competition, predation, and physiological tolerance (Begon et al. 1990, Stearns 1992, Roff 2002). Understanding how environmental and biological factors affect 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, dramatic environmental changes occurred in the marine environment including rising temperature, lowering pH, and frequent severe events such as extreme high temperature, torrential rains, and droughts (Houghton et al. 2001, Caldeira & Wickett 2003, Solomon et al. 2007). The climate-driven environmental changes have shown significant impacts on the health and function of organisms, severely affect biodiversity, and eventually alter community structure and ecosystem functions (Riebesell et al. 2000, Hoegh-Guldberg et al. 2007, Allen et al. 2010). Investigations at species levels have revealed complex patterns of organisms in relation to climate changes across multiple taxa (Stillman & Somero 2000, Ries et al. 2009). Organisms within one population often display diverse individual responses to environmental conditions (Båmstedt 1988, Marras et al. 2010, Fodrie et al. 2015). These

differences may reflect in growth, development, mortality and reproduction, which in turn affect population structure and sustainability (Clark 2003).

Individuals are the building blocks of ecological systems and individual variation is the basis of natural selection theory (Grimm & Railsback 2013). Under increasing environmental stress, individuals that are more adaptive to the environment can achieve higher fitness and have larger probability of passing genes to next generations. For example, rapid growth allows individuals to pass the period of high mortality at the early life stages quickly, resulting in increased survival, younger age at maturity, and increased egg production (Roff 2002). Recent studies have shown that some populations may adapt to climate change via natural selection acting on existing individual variations (Hoffmann et al. 2003, Balanyá et al. 2006, Pistevos et al. 2011). More adaptive individuals within a population could adapt to a wide range of environmental conditions (Rice et al. 1993). Individuals with higher fitness are selected resulting in diversified population structures under various environmental conditions and increased population sustainability when the species experiencing environmental stressors (Nussey et al. 2007). It has been proposed that populations under unfavorable environmental conditions show a greater degree of individual variability (Warwick & Clarke 1993, Pfister & Stevens 2002). Presumably, populations with higher level of individual variability would be more resilient and resistant to environmental changes, and consequently have higher chances to survive.

The need for knowledge on individual variability and population adaption has led to the rise of individual-based model (IBM) approaches. Traditional population models

(e.g., exponential growth) are largely built upon an assumption that all individuals in a population have identical life history parameters, thereby these models center on aggregate life history parameters at population levels, such as growth and mortality (Malthus 1798). Stage- or age-structured models allow the vital rates to vary among classes, but individuals within each class are still treated as the same (Leslie 1945, Caswell 2001). Methodologically, the structured modeling approach has been extended to the IBM approach at individual levels, by endowing each individual with unique physiological traits (Batchelder & Miller 1989, Batchelder & Williams 1995). The effects of environmental factors on each individual are distinct, but ultimately these effects are integrated to form observed overall variations in the population (Grimm & Railsback 2013). Despite IBM, as a typical modeling approach, has been widely applied to test the effects of variability in a series of intrinsic and extrinsic factors on organisms (Letcher et al. 1996, Rose et al. 1999), studies on the interactive effects of individual variability and extrinsic factors on dynamics at population levels remain insufficient (Rice et al. 1993, Richmond et al. 2013). To improve the understanding of individual variability on population dynamics, we developed an IBM model to test the role of variations in physiological traits among individuals in sustaining populations under different environmental conditions.

By focusing on a widely distributed coastal copepod species (*Acartia tonsa*) we used the IBM model to examine the impacts of individual variability in physiological parameters on population dynamics under different environmental factors including temperature, salinity, and chlorophyll (Chl) *a* as a proxy for food concentration. There

has been lots of research on the effects of multiple environmental factors on zooplankton (e.g. Kleppel 1992, Dagg 1997); to get a complete output, we still included environmental effects in the results. The model followed the life history of a copepod, i.e., egg, six naupliar stages, five copepodite stages and adult. *A. tonsa* is a numerically abundant copepod species in the coastal Gulf of Mexico, and consists of an important prey for gelatinous zooplankton and larval fish (Ortner et al. 1989, Checkley et al. 1992, Elliott et al. 2012). We hypothesized that population of *A. tonsa* may benefit from a relatively high level of individual variability under adverse environmental stresses. Specifically, we quantified the impacts of abiotic and biotic factors on the population dynamics of *A. tonsa* to understand the role of individual variability in sustaining populations under varying environmental conditions, and identify key factors governing the population dynamics of this species. Findings from our IBM approach will be useful to advance the understanding of marine food web dynamics and forecast the effects of environmental changes on pelagic communities in the ocean.

2. METHODS

2.1 Model species and the physical environment

A. tonsa widely exists in majors oceans (Atlantic, Indian, Pacific), their marginal seas (Baltic, Black , Caspian, Mediterranean, North, Gulf of Mexico), and other nearshore marine environments such as bays and estuaries (Mauchline 1998, Gonzalez 2013, Walter & Boxshall 2015). Physiologically, *A. tonsa* can tolerate a wide range of water temperature (-1 to 32 ºC) and salinity (1 to 38), and can survive sudden changes in environmental conditions (Gonzalez 2013). Growth, reproduction and survival of *A. tonsa* are subjected to food availability, predation, salinity, and temperature (Berggreen et al. 1988, Purcell et al. 1994, Zhang et al. 2014, Peck et al. 2015).

Galveston Bay, one of the largest estuarine systems along the northern Gulf of Mexico coast, supports numerous marine taxa including fishes, shrimps, crabs and oysters (CHF 2010, Gilmer et al. 2012), and has been subjected to impacts from human and natural stressors for decades (Lester & Gonzalez 2003). The complex water system in Galveston Bay provides various environmental conditions to examine population dynamics of *A. tonsa* in response to environmental changes. For example, summer temperature regularly exceeds 32 °C and winter temperature is as high as ~16 °C and as low as ~4 °C (The Weather Channel 2015). Salinity is affected by the seasonal freshwater inflow exhibiting large spatial and temporal variations with the inner bay relative to regions near the tidal pass (Orlando 1993, Buzan et al. 2009, Quigg 2011). Chl α concentration also shows a strong seasonality with a peak occurring regularly in

March-April in most part of the Bay (Santschi 1995), and often respond quickly to nutrient pulses from freshwater by increasing phytoplankton growth and biomass (Örnólfsdóttir et al. 2004).

I used the IBM to simulate population abundance, egg production, and stage structure over 100 days under a range of environmental conditions typical to Galveston Bay. I also assigned different variations on physiological traits among individuals and explored population dynamics under different environmental conditions. In total, three simulation experiments were conducted. Experiment 1 examined effects of individual variability on population dynamics under different temperatures, with favorable salinity and food concentration. Experiment 2 examined effects of individual variability on population dynamics under different food concentration, with favorable temperature and salinity. Experiment 3 examined effects of individual variability on population dynamics under different salinity, with favorable temperature and food concentration. For each experiment, a generalized additive model (GAM) was applied to examine the overall effects of the corresponding environmental factor and individual variability on population persistence of *A. tonsa*. Finally, a multiple regression model was developed to compare the relative effects of the three environmental factors and individual variability on population survival.

2.2 Description of IBM

Four biological processes including growth, development, reproduction, and mortality were mathematically formulated in the IBM model (Figure 1). The model tracked a population of *A. tonsa* over a period of 100 days (d) with a time step of 0.1 d. Most copepod taxa have an entire life cycle from egg hatching to adult as short as ~2-3 months or even shorter for trophic species (Mauchline 1998). A period of 100 d ensured at least one generation could be realized. The model was simulated 100 times under each environmental condition. Growth was divided into growth in body carbon and growth in molt carbon. Growth rate was dependent on food concentration, body weight and temperature. When molt carbon exceeded a threshold value, individuals molted to the next stage, i.e., development occurred. Copepods have a rigid, 13-stage life history pattern (i.e. egg, six naupliar stages, five copepodite stages and adult), so there were 11 threshold values for molting (there was no molt threshold for egg stage). Once mature, all assimilated carbon except metabolism was devoted to body carbon that was further broken into tissue carbon and gonad carbon, and molt carbon was set as zero. Daily egg reproduction (# of egg per female per day) was computed from net gained gonad carbon weight, which was estimated as a proportion of the growth of body carbon. Mortality was set as weight-dependent (Peterson & Wroblewski 1984, McGurk 1986). In the model, all individuals started from the first naupliar stage (N1). The functions of growth and development were modified from publications (Van Den Bosch & Gabriel 1994, Richmond et al. 2013).

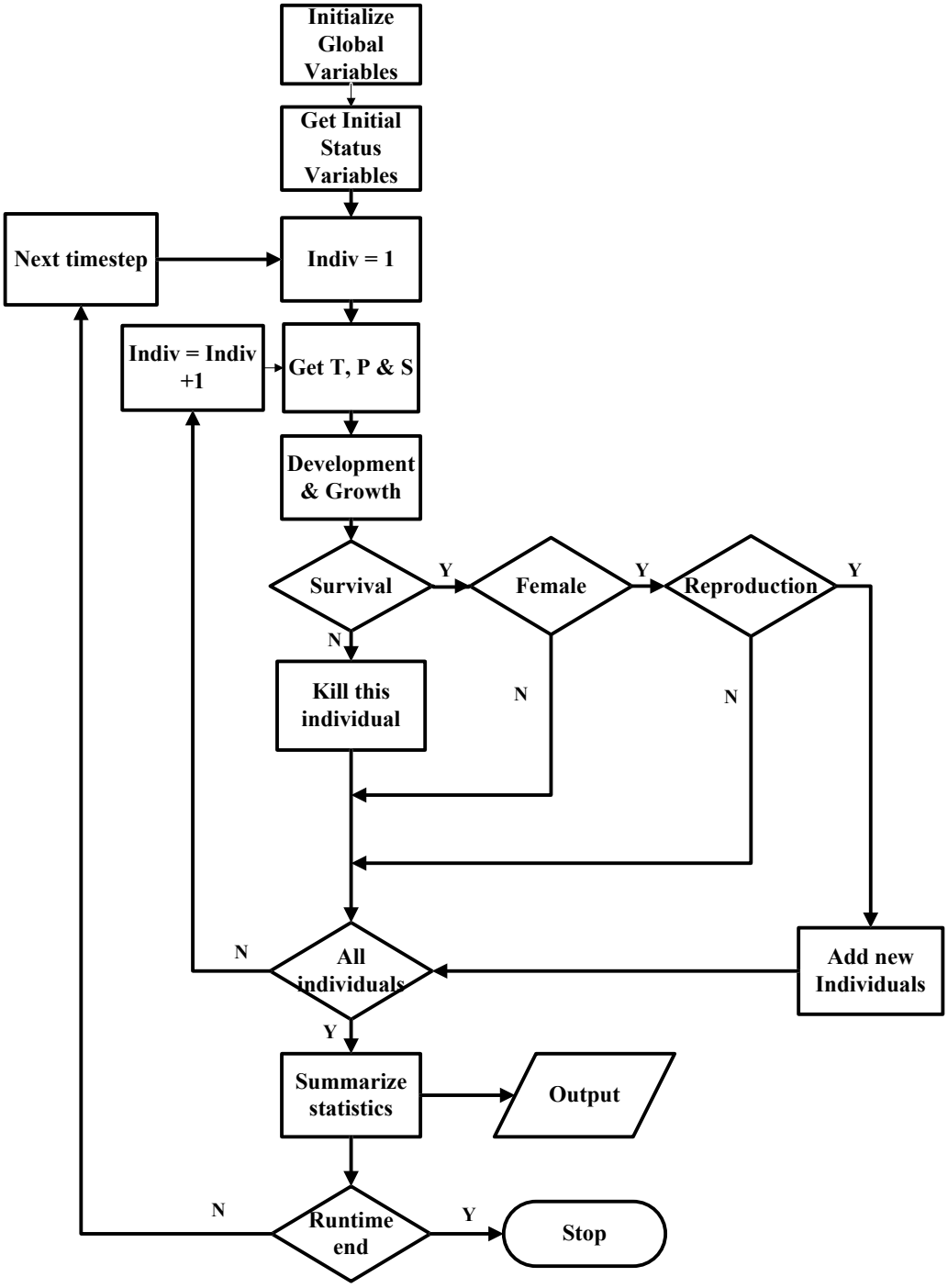

Figure 1. Flow chart for the individual-based model of *A. tonsa* population. The flow chart showed each of the events that could happen to an individual during its life: growth, development, reproduction and survival.

2.2.1 Growth and development

Growth at stage *i* was allocated to two pools: body carbon (W_i, µgC) and molt carbon (S_i, µgC). Daily growth of body carbon (ΔW_i) and molt carbon (ΔS_i) were the differences between assimilation and metabolism. Metabolic losses were assumed proportional to the body and molt carbon pools respectively.

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

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

where k is the fraction of assimilated carbon that goes to body carbon, A is assimilated carbon (µgC d^{-1}), β_1 and β_2 are metabolic costs as a proportion of body and molt carbon (d^{-1}) (values in Table 1).

Assimilated carbon (A) was a function of temperature, food concentration and body weight (Batchelder & Williams 1995):

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

where I_{max} is maximum ingestion rate (µgC d^{-1}), α is a shape parameter of the functional response relationship (µgC^{-1}), θ is a shape parameter for the effect of body weight on maximum ingestion, P is the food concentration (µgC L^{-1}), γ is the assimilation efficiency (values in Table 1).

Table 1. Parameters used in the individual-based model.

Variable	Description	Units	Value	Source
I_{max}	Maximum ingestion rate	μgC (μgC copepod)$^{-1}$ d^{-1}	1.209	Richmond et al. 2013
α	Shape parameter of the functional response	μgC^{-1}	0.00675	
θ	Shape parameter for the effect of body weight on maximum ingestion		0.850	
γ	Assimilation efficiency		0.504	
β_1	Metabolic costs as a proportion of body carbon	d^{-1}	0.132	
β_2	Metabolic costs as a proportion of molt carbon	d^{-1}	0.132	
k	Fraction of assimilated carbon accumulated as body carbon		0.866	
W_{min}	The minimum body weight for female to start to reproduce	μgC	3.24	Durbin et al. 1983
W_{max}	The maximum body weight for female to devote all assimilated energy to egg production	μgC	7.30	
E_{ep}	Transformation efficiency between gonad weight and eggs	$\begin{cases}\min(-0.2408+0.0267\times T^*, 1.0) & (T \le 24)\\ \max(0.4-0.0488\times(T-24), 0) & (T > 24)\end{cases}$		Holste and Peck 2006

* T stood for temperature.

An individual molted to next stage when its molt carbon (S_i, µgC) exceeded a threshold value (ST_i, µgC, values in Table 2). Once molting, molt carbon was reset to zero. The process of feeding, assimilation, buildup of carbon for the next molt, and molting kept being repeated until the individual reached the adult stage.

Table 2. *Acartia tonsa* molt carbon threshold (*ST*) in each stage.

Stage	Molt carbon threshold (ST, µgC)	Source
N1*	0.0138	Richmond et al. 2013
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	

* N = naupliar, C = copepodite.

2.2.2 Reproduction

Offspring production of adult females completes individual life history and the offspring number determines the initial population abundance of the next generation. When a female individual grew to adult stage, all assimilated carbon in excess of metabolism was devoted to body carbon (W, µgC), which was divided into two parts: tissue carbon (W_S, µgC) and gonad carbon (W_E, µgC) (Hirst & McKinnon 2001). The

proportion of mass accumulation in gonad carbon to body carbon (f_E) was a function of body carbon:

$$f_E = \begin{cases} 0\ (W < W_{min}) \\ \frac{W - W_{min}}{W_{max} - W_{min}}\ (W_{min} \le W \le W_{max}) \\ 1\ (W > W_{max}) \end{cases} \quad \text{(Eq. 4)}$$

where W is body carbon weight, W_{min} is the minimum body weight for female to start reproduction, W_{max} is the maximum body weight for female to devote all assimilated energy to egg production (values in Table 1).

Daily egg production of single female was computed using net gained gonad carbon divided by an average weight of an egg, then multiplied by a temperature-dependent transformation efficiency between gonad weight and eggs (E_{ep}, equations see Table 1). An mean value of 0.035 μgC egg^{-1} was utilized (Ambler 1985, Richmond et al. 2013). Eggs produced within one day were taken as one clutch, and an individual female may produce a maximum of 20 clutches during her lifetime (Mauchline 1998).

Hatching success (*HS)* of newly produced eggs was a function of temperature (T) and salinity (S). The effects of temperature and salinity are confounding, here, I formulated the effects of temperature and salinity reported by Holste & Peck (2006).

$$HS = \frac{3.8 \times T + 5.73}{100} \times \left(\frac{62.74}{1 + e^{-0.44 \times (S - 6.63)}} + 25.25\right) \div 100 \quad \text{(Eq. 5)}$$

Newly produced eggs needed a short period to hatch before recruiting to populations. Hatching time (*HT)* was considered as a function of temperature (Holste & Peck 2006).

$$HT = -1.84 \times T + 64.34 \quad \text{(Eq. 6)}$$

2.2.3 Mortality

Stage-specific mortality rate is a major factor governing copepod population dynamics, and subjected to temperature, food, predation and population density etc. (Ohman 1986, Ohman & Hirche 2001). Among these factors, predation on average accounts for up to 60-75% of the total mortality (Hirst & Kiørboe 2002).

Another form of mortality to be considered is cannibalism due to the feeding from adult and late copepodite stages on eggs (Roman 1977, Lemus 2006). A density-dependent cannibalism effect of C4, C5 and adult cannibalism on eggs was incorporated 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):

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

where M_{egg} is egg mortality (d^{-1}), *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). As a result, egg mortality was adjusted by $Q_{10}^{\frac{T-T_{ref}}{10}}$, where Q_{10}= 1.3, T_{ref} = 15 (Hirst & Kiørboe 2002). While egg mortality rate is density dependent at high adult abundance, it is independent of population density when adults are at low abundance (Ohman et al. 2002). Consequently, egg mortality was reset to 0.5 when it was lower than 0.5 due to low C4s, C5s and adult abundance (Wang et al. 2014). At each time step, the number of survival

eggs was reduced exponentially (Eq.8, according to Fager 1973). After a hatching period, eggs surviving to N1s were added to the simulated population.

$$N_{t+\Delta t} = N_t \times e^{-Megg \cdot \Delta t} \quad \text{(Eq. 8)}$$

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

Stage specific mortality varies among different developmental stages. In general, mortality rates of marine pelagic organisms decrease with increasing body size (Peterson & Wroblewski 1984, Miller et al. 1988), which leads to larger or faster growing individuals gaining a survival advantage over smaller conspecifics via a shortened duration in the more vulnerable size classes to predators and better tolerance of extreme environmental conditions (Houde 1997). Therefore, a weight dependent mortality was adopted for naupliar (N1 to N6), copepodite (C1 to C5) and adult stages (Eq. 9). In my model, except egg stage, mortality (M) was formulated to decrease with increasing dry body weight (W_{dry}, g) (Peterson & Wroblewski 1984):

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

I calculated dry body weight by assuming that the carbon content was 40% of dry weight based on the findings of carbon contents ranging from 35.2 to 47.6% for mixed copepods in the Sargasso Sea (Beers 1966). Although the mortality scaled as -0.25 power of dry weight was derived from data of juvenile and adult fish only (Peterson & Wroblewski 1984), it was proved 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 the Q_{10}term. Each individual was evaluated at each time step for whether it survived or died. A uniform random number between 0 and 1 was generated, and if the random number was less than its mortality, the individual died and was removed from the simulation (Batchelder & Williams 1995, Batchelder et al. 2002).

2.3 Initial condition and individual variability

Each simulation began with 100 individuals of first-stage nauplii (N1). Initial molt carbon (S_0) was set to zero for all individuals. Initial body carbon (W_0) was set using a normal distribution with mean (μ) = 0.2 μgC (Richmond et al. 2013), standard deviation (SD) = 10% × μ, and minimum and maximum values were set as $\mu \pm 2$ SD.

I assigned the four physiological parameters I_{max}, α, β_1 and β_2 assumed normally distributed by defining mean values and SDs, respectively. Mean values were computed using the calibrated values (Richmond et al. 2013). Individual variability (IV) was defined as coefficient of variation (CV) represented as SD/mean×100%. SDs were calculated based on mean and IV (SD = mean × IV) in turn. The four parameters were assigned to individuals in a related format: I_{max} was positively correlated with α, and negatively correlated with β_1 and β_2 (Richmond et al. 2013). An individual with higher I_{max} and α but lowerβ_1 and β_2 is an efficient feeder and fast-grower. For each simulation, each individual was assigned a coefficient following a standard truncated normal distribution (μ = 0, SD = 1, maximum and minimum values = $\mu \pm 2$ SD). Each physiological parameter of an individual was computed as the coefficient times the SD of the parameter plus the corresponding mean value. I used the same coefficient for I_{max}

and α, but the negative coefficient for β_1 and β_2 to set a positive correlation between I_{max} and α and a negative correlation between I_{max} and β_1 and β_2. In this way, each parameter followed a normal distribution, but all four parameters were completely correlated. I_{max}, α, β_1 and β_2 were adjusted with $Q_{10}^{\frac{T-T_{ref}}{10}}$ for all temperatures. All parameters values were assumed to be appropriate for 18 ºC, so T_{ref} was set as 18 ºC (Richmond et al. 2013).

2.4 Simulation experiments

2.4.1 Factorial experimental design

Factorial experimental design was applied to test the effect of IV on abundance, egg production and population survival under different environmental conditions. Four factors including temperature, food concentration, salinity and IV were combined to conduct these experiments.

Annual sea temperature in Galveston Bay ranged from 12 to 32 ºC from 2006 to 2012 (NOAA Buoy Station GTOT2 & GNJT2). The Bay showed moderate or low phytoplankton biomass, with typical values of 13-17 µg Chl *a* L^{-1} in upper Bay (Strong 1977, Krejci 1979, Smith 1983) and 3.8-14.6 µg Chl *a* L^{-1} in the middle to lower Bay (Santschi 1995). The Chl *a* was converted into carbon content to represent food concentration in the model. Salinity affected by freshwater inflow showed large spatial and temporal variations ranging from 0 to 35 (Orlando et al. 1993). As a result, six temperature levels (12, 16, 20, 24, 28, 32 ºC), eight food concentration levels (100, 200, 300, 400, 500, 600, 700, 800 µgC L^{-1}), and eight salinity levels (0, 5, 10, 15, 20, 25, 30,

35) were adopted in my simulation experiments. These environmental conditions were representative of a year-around pattern encountered by *A. tonsa* in Galveston Bay. Some proper combinations of the three environmental factors could be considered typical conditions of Galveston Bay at different time of the year when *A. tonsa* is present. The optimal temperature for egg production of *A. tonsa* was found within 22.9 and 24.8 ºC (Holste & Peck 2006), so 24 ºC was considered the most favorable temperature in this study. Previous laboratory studies demonstrated that growth rate (Paffenhofer 1976), and egg production rate (Durbin et al. 1983) of copepods are positively related to food availability, and consequently, the highest food concentration level (800 μgC L^{-1}) was taken as the most favorable food condition. Hatching success of *A. tonsa* was reported increased with increasing salinity for a Baltic population and salinity of 35 was selected as the most favorable condition (Holste & Peck 2006).

The magnitude of IV was set as the CV of the four parameters (I_{max}, α, β_1 and β_2). Six levels of IV (0, 10%, 20%, 30%, 40%, 50%) were used in this study. Based on previous studies, variability of 20% to 30% is a common degree of variability in bioenergetic traits such as ingestion and metabolic rates in natural copepod populations (Båmstedt 1988, Richmond et al. 2013), so the range used here set them in the middle. Overall, there were 6×8×8×6 treatment combinations in total. The effects of IV on population dynamics of *A. tonsa* under single variable environmental factor were tested in two-factor factorial experiments (Experiment 1, 2, 3 in Table 3). Additionally, the multiple factorial experiment (Experiment 4 in Table 3) allowed me to test the relative importance of each factor on regulating population dynamics of *A. tonsa*.

Table 3. Simulation experiments design.

Factors		Experiments				Factors		Experiments			
		1	**2**	**3**	**4**			**1**	**2**	**3**	**4**
T*	12	+	-	-	+	**IV***	0	+	+	+	+
	16	+	-	-	+		10	+	+	+	+
	20	+	-	-	+		20	+	+	+	+
	24	+	+	+	+		30	+	+	+	+
	28	+	-	-	+		40	+	+	+	+
	32	+	-	-	+		50	+	+	+	+
P*	100	-	+	-	+	**S***	0	-	-	+	+
	200	-	+	-	+		5	-	-	+	+
	300	-	+	-	+		10	-	-	+	+
	400	-	+	-	+		15	-	-	+	+
	500	-	+	-	+		20	-	-	+	+
	600	-	+	-	+		25	-	-	+	+
	700	-	+	-	+		30	-	-	+	+
	800	+	+	+	+		35	+	+	+	+

* T = temperature, P = food concentration, S = salinity, IV = individual variability, "+" = presence in the experiment, "–" = absence.

2.4.2 Analytical methods

For each double factorial experiment (Experiment 1, 2, 3), two-way analysis of variance (ANOVA) was conducted to test the effects of the corresponding environmental factor and IV on population abundance and egg production. Then a generalized additive model (GAM) was applied to test the comprehensive effects of environmental factor and IV on population survival, which was represented by survival ratios of 100 simulations. GAM is advantageous when the relationship between dependent variable and independent variable is nonlinear (Hastie & Tibshirani 1990). Instead using predictors

multiplied by the coefficients directly, GAMs incorporate smooth functions s(x) of at least some (possibly all) covariates (Wood 2006). Akaike's information criterion with a correction for finite sample sizes (AICc) was adopted as the criteria to select the best GAM (Burnham & Anderson 2002).

In the multiple 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).

3. RESULTS

3.1 Experiment 1: Individual variability and temperature

Temperature had significant influence on population abundance ($F_{5, 3564}$ = 34323.41, $p < 0.01$, Figure 2a) and egg production ($F_{5, 3564}$ = 296371.80, $p < 0.01$, Figure 2b). Abundance (Figure 2a) and egg production (Figure 2b) were higher in the intermediate temperature levels (24 and 28 ˚C) than high (32 ˚C) and low (12 ˚C) levels. 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. Higher temperature led to faster growth (Figure 3a) and higher mortality (Figure 3b). At low temperature transfer efficiency between gonad weight and eggs increased as temperature increased, and peaked around 24 ˚C, and then decreased as temperature increased (Figure 3c). Hatching success increased as temperature increased (Figure 3d).

IV had significant effects on abundance ($F_{5, 3564}$ = 769.67, $p < 0.01$, Figure 2a), and temperature and IV had a significant interaction ($F_{25, 3564}$ = 121.37, $p < 0.01$). Abundance increased with increasing IV except at 24 ˚C, and the increases were larger at unfavorable temperature levels (12 and 32 ˚C) than favorable settings. At 12 ˚C, mean abundance was the same (zero) when IV ranged from 0 to 30%, but when IV increased from 40% to 50% mean abundance showed about 6-fold increase (24.96 at IV = 40% to 156.95 at IV = 50%, $F_{1,198}$ = 148.11, $p < 0.01$). At 32 ˚C, mean abundance increased from 0.99 at IV = 0 to 206.59 at IV = 50%, and IV had significant effect on abundance ($F_{5, 594}$

= 1509.10, $p < 0.01$). However, at 24 ˚C, not all IVs were significantly different from others (e.g. $F_{1,198} = 2.02$, $p > 0.1$ between IV = 10% and 20%), and mean abundance decreased 3% from IV = 0 to 50% (581.70 at IV =0 to 564.81 at IV = 50%).

IV exhibited a significant effect on egg production ($F_{5, 3564} = 48576.20$, $p < 0.01$, Figure 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 temperatures. Mean egg production when IV varying from 0 to 50% was about 65 times higher at 12 ˚C (93.37 at IV = 0 to 6023.30 at IV = 50%) and about 187 times higher at 32 ˚C (52.00 at IV = 0 to 9677.65 at IV = 50%), but only about 3 times higher at 24 ˚C (202536.20 at IV = 0 to 685502.20 at IV = 50%) and 28 ˚C (156774.30 at IV = 0 to 534860.70 at IV = 50%).

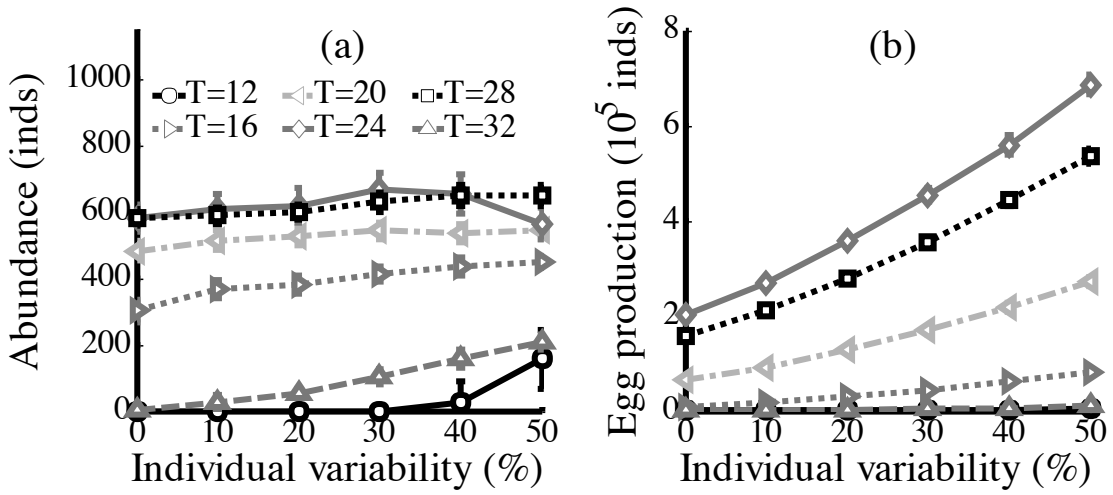

Figure 2. Experiment 1: (a) mean abundance and (b) mean egg production over 100 simulations for different degrees of individual variability (IV) under different temperature levels. Each error bar represented the standard error over the corresponding 100 simulations. All simulations were performed under favorable food concentration (800 µgC L^{-1}) and favorable salinity (35).

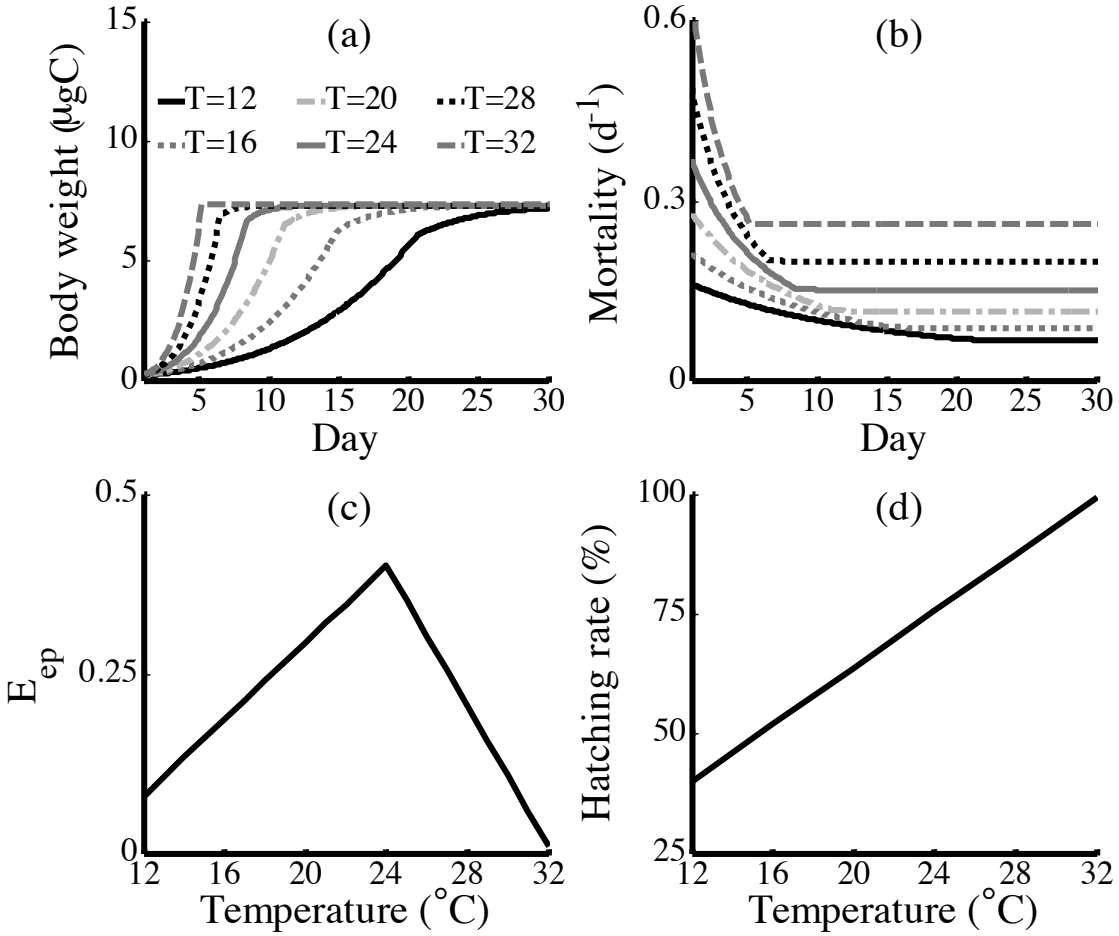

Figure 3. Experiment 1: a typical simulation showing (a) daily growth of body weight of an individual, (b) daily mortality of an individual, (c) transformation efficiency between gonad weight and eggs (E_{ep}), and (d) hatching rate under different temperature levels. The individual was assigned mean values of the four physiological traits (I_{max} = 1.209, α = 0.00675, β_1 = 0.132, β_2 = 0.132, see Table 1 for the definition of the four traits). Simulation was performed under favorable food concentration (800 µgC L^{-1}) and favorable salinity (35).

The effect of IV on population abundance and egg production was due to the selection on faster growing individuals with higher ingestion rates (larger I_{max} and larger α) and lower metabolism rates (smaller β_1 and β_2) (Figure 4a-d). For example, at 24 ˚C, the average I_{max} and α 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%, Figure 4a, α = 0.0067 at IV = 0 to 0.0085 at IV =50%, Figure 4b), while the average β_1 and β_2 values decreased 26% from IV = 0 to 50% (0.13 at IV = 0 to 0.10 at IV = 50%, Figure 4c, d). Faster growth benefited individuals by allowing them to pass quickly through the vulnerable early life stages, resulting in earlier maturation (Figure 4e), a larger proportion of adults (Figure 4f), and higher daily egg production (Figure 5a-f), which led to higher overall egg production.

The final GAM showed that both temperature and IV exhibited significant effects on population survival ($p < 0.01$). The effect of temperature peaked around the optimal values (24 to 28 ˚C), and tapered off at low and values (Figure 6a). The estimated degree of freedom (edf) of temperature was 2.1, representing a 2.1^{st}-degree polynomial needed to reproduce the spline. IV and survival were positively correlated, because the effect of IV increased with increasing IV (Figure 6b). The edf of IV was 1.85, implying the relationship between IV and survival was not linear. Under unfavorable temperature, survival was low at IV = 0, and improved as IV increased (Figure 6c). At IV = 0, to get a 100% survival, temperature should be ranged from 16 to 30 ˚C. When temperature was 32 ˚C, to survive 100%, IV should be above 29%.

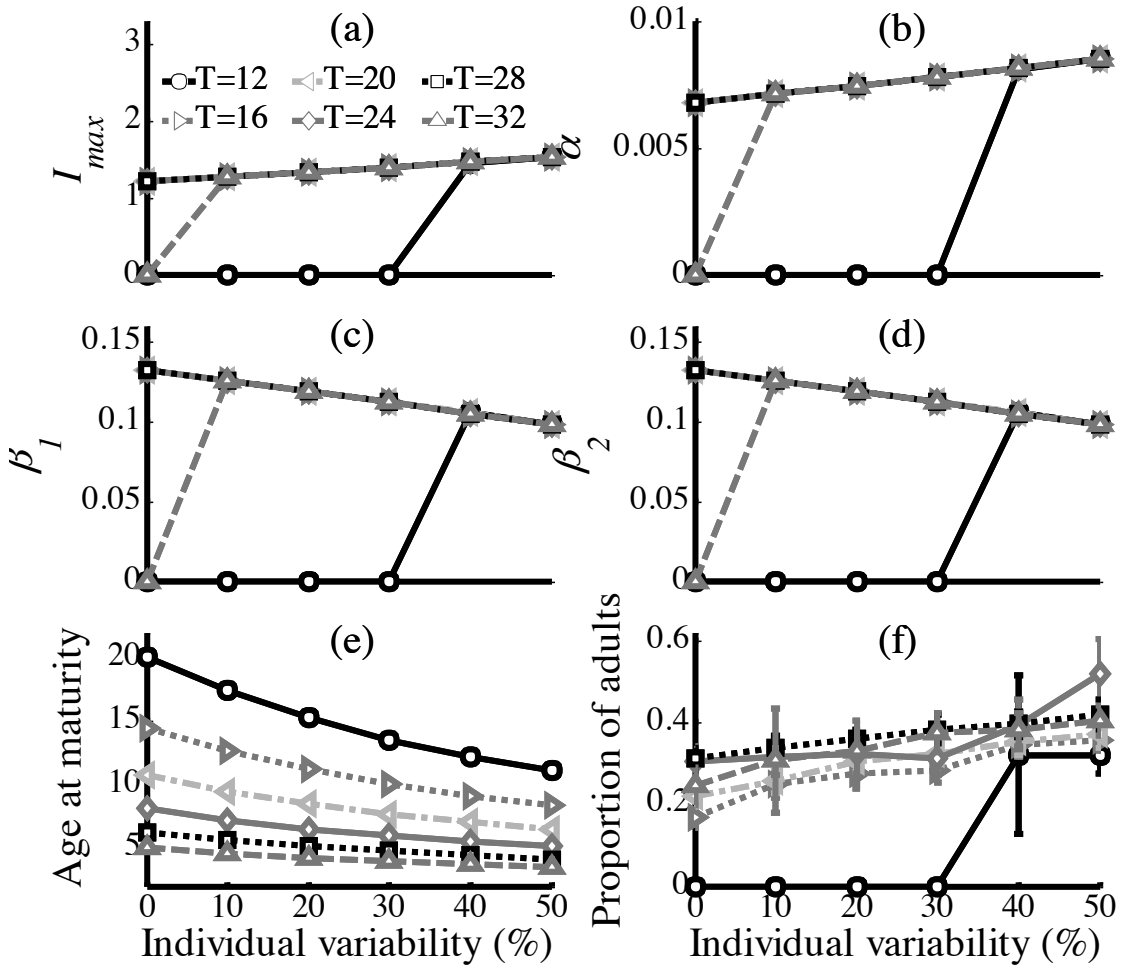

Figure 4. Experiment 1: (a-d) mean traits of survivors over 100 days, (e) mean age at maturity of the original individuals, and (f) mean proportion of adults over 100 days over 100 simulations for different degrees of IV under different temperature levels. Error bars represented standard errors over 100 simulations. See Table 1 for the definition of the four traits. The values of zero for the four traits implied that there was no survivor. All simulations were performed under favorable food concentration (800 μgC L^{-1}) and favorable salinity (35).

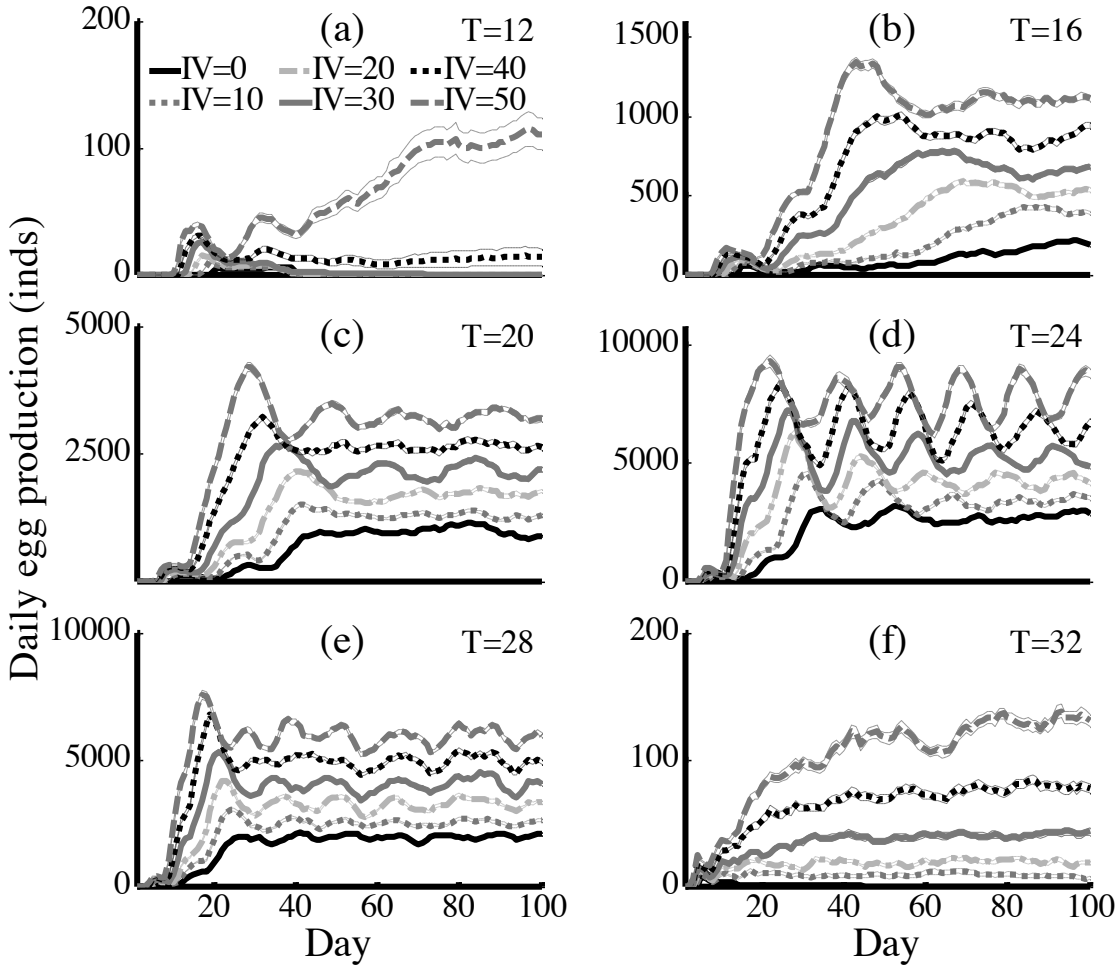

Figure 5. Experiment 1: mean daily egg production over 100 simulations for different degrees of IV under different temperature levels. The thinner lines showed the 95% confidential intervals. All simulations were performed under favorable food concentration (800 µgC L^{-1}) and favorable salinity (35).

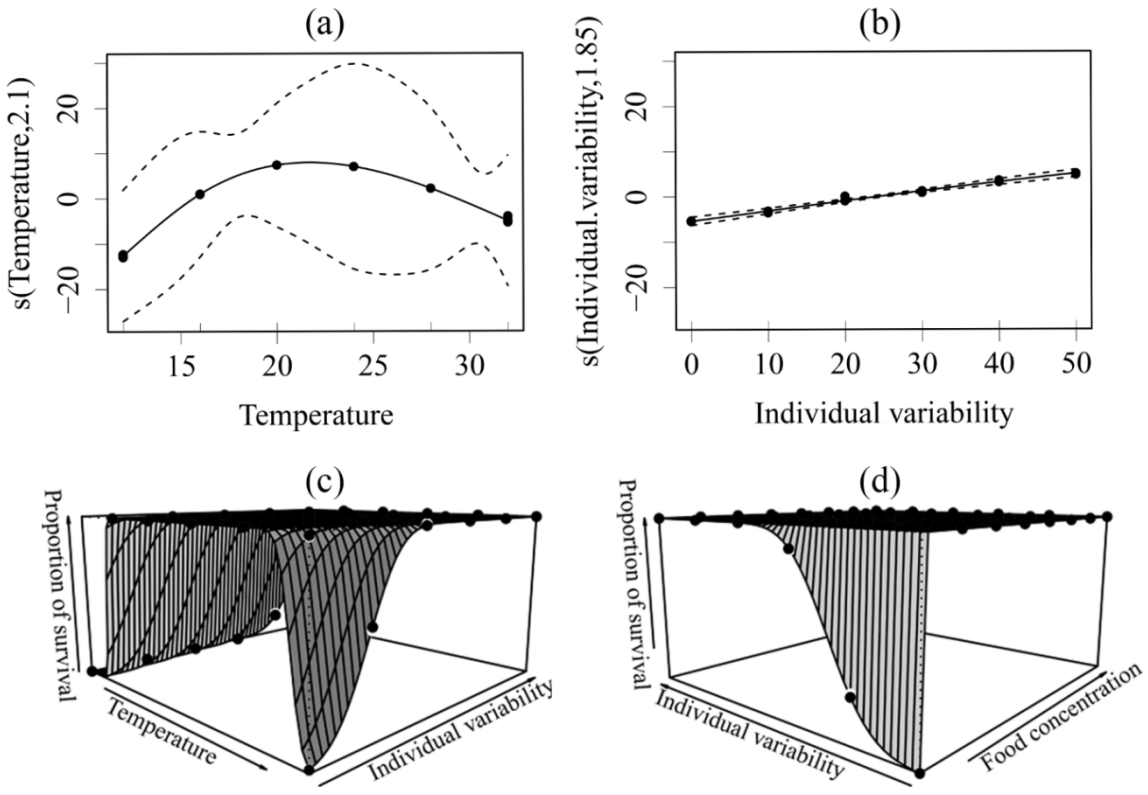

Figure 6. Experiment 1: (a, b) partial-regression plots of GAM that modeled population survival (i.e. survival ratio in 100 simulations) with IV and temperature. A plot of of x versus s(x) shows the relationship between x and y holding constant the other variables in the model. The number appearing in the smooth term was called as estimated degree of freedom (edf). Experiment 1: (c) three-dimensional plots examining the relationship among population survival, IV and temperature. Experiment 2: (d) three-dimensional plots examining the relationship among population survival, IV and food concentration.

3.2 Experiment 2: Individual variability and food concentration

The impacts of food concentration were significant on population abundance ($F_{7, 4752} = 2029.50$, $p < 0.01$, Figure 7a) and egg production ($F_{7,4752} = 68203.60$, $p < 0.01$, Figure 7b). Abundance and egg production were lower under the lowest food concentration (100 μgC L^{-1}) than others, especially when IV was less than 30%. These effects were resulted from the influence of food concentration on growth rate and weight-dependent mortality. Under higher food concentrations, individuals tended to grow faster with high body weight (Figure 8a), resulting in lower mortality (Figure 8b).

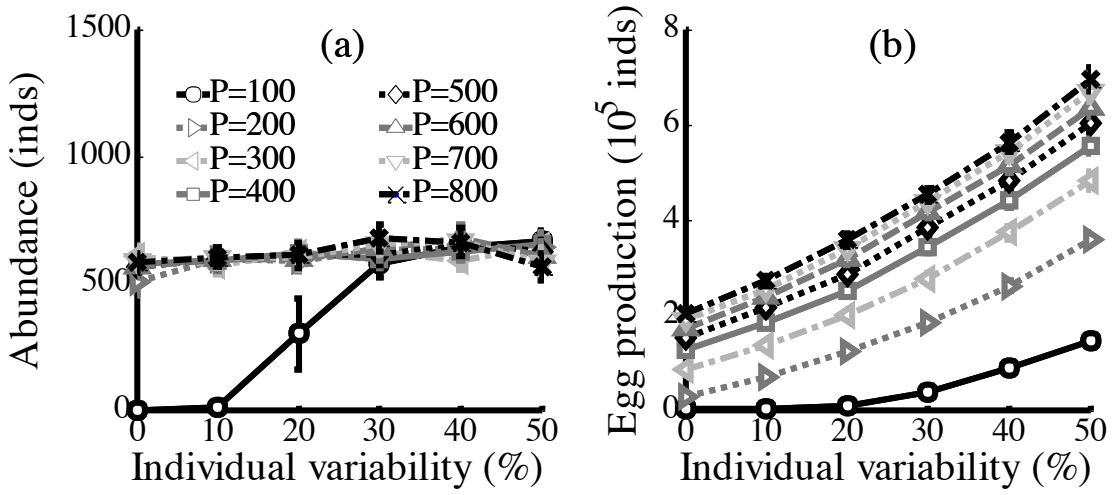

Figure 7. Experiment 2: (a) mean abundance and (b) mean egg production over 100 simulations for different degrees of IV under different food concentration levels. Each error bar represented the standard error over the corresponding 100 simulations. All simulations were performed under favorable temperature (24 ºC) and favorable salinity (35).

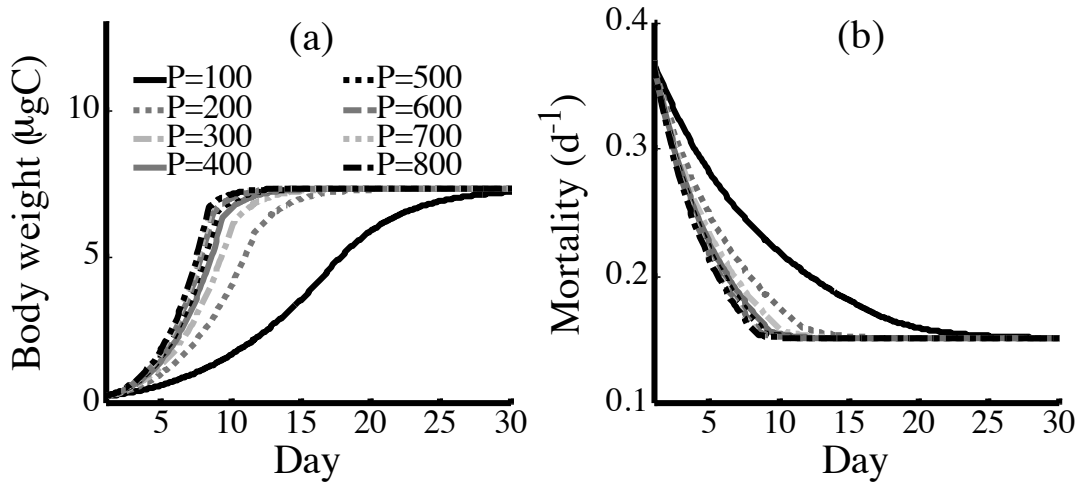

Figure 8. Experiment 2: a typical simulation showing (a) daily growth of body weight of an individual, (b) daily mortality of an individual under different food concentration levels. The individual was assigned mean values of the four physiological traits (I_{max} = 1.209, α = 0.00675, β_1 = 0.132, β_2 = 0.132, see Table 1 for the definition of the four traits). Simulation was performed under favorable temperature (24 ºC) and favorable salinity (35).

IV had significant effects on abundance ($F_{5, 4752}$ = 1275.26, $p < 0.01$, Figure 7a), under low food concentration in particular ($F_{35, 4752}$ = 463.69, $p < 0.01$). For instance, at 100 µgC L^{-1}, abundance increased with increasing IV dramatically ($F_{5, 584}$ = 1893.00, $p < 0.01$), and the effect of each IV differed from the others significantly (e.g. $F_{1, 198}$ = 24.67, $p < 0.01$ between IV = 0 and 10%; $F_{1, 198}$ = 29.42, $p < 0.01$ between IV = 40% and 50%). Mean abundance when IV ranging from 10% to 50 % increased about 46 times (14. 09 at IV = 10% to 668.69 at IV = 50%). In contrast, at 200 µgC L^{-1}, 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 ($F_{5, 4752} = 120961.40$, $p < 0.01$, Figure 7b), 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. Mean egg production increased as high as 37517 times from IV = 0 to 50% at 100 μgC L^{-1} (3.85 at IV = 0 to 144439.60 at IV = 50%), but only about 14 times at 200 μgC L^{-1} (25923.99 at IV =0 to 358564.15 at IV = 50%), and even less under higher food concentrations.

Environmental selection preferred effective grazers with greater assimilation rates and smaller metabolism rates (Figure 9a-d). As IV increased, more individuals displayed greater I_{max} and α, and smaller β_1 and β_2. At 100 μgC L^{-1}, the average I_{max} value and α 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%, Figure 9a, α = 0.0071 at IV = 0 to 0.0085 at IV = 50%, Figure 9b); the average β_1 and β_2 values decreased 22% (0.13 at IV = 10% to 0.10 at IV = 50%, Figure 9c, d). Consequently, effective grazers had faster growth rates, leading to earlier maturation (Figure 9e), more adults (Figure 9f), and higher daily egg production (Figure 10a-f).

The GAM including an interactive effect between food concentration and IV was chosen as the best model, and the interaction term was significant ($p < 0.01$). Except for 100 μgC L^{-1}, populations under all other concentration levels survived absolutely (Figure 6d). The required food concentration to survive one hundred percent of the population when IV = 0 was 106 μgC L^{-1}. Under 100 μgC L^{-1}, IV should be above 34% to get 100% survival.

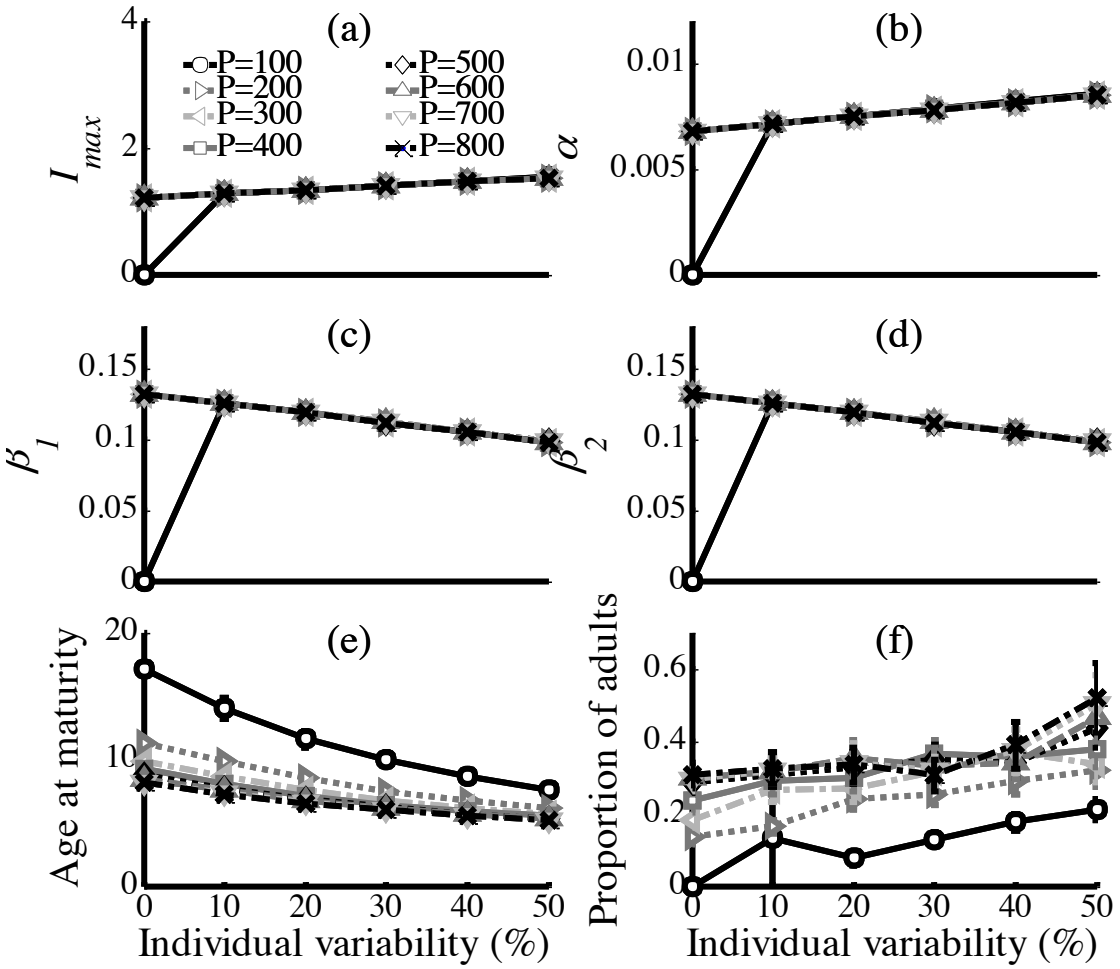

Figure 9. Experiment 2: (a-d) mean traits of survivors over 100 days, (e) mean age at maturity of the original individuals, and (f) mean proportion of adults over 100 days over 100 simulations for different degrees of IV under different food concentration levels. Error bars represented standard errors over 100 simulations. See Table 1 for the definition of the four traits. The values of zero for the four traits implied that there was no survivor. All simulations were performed under favorable temperature (24 ºC) and favorable salinity (35).

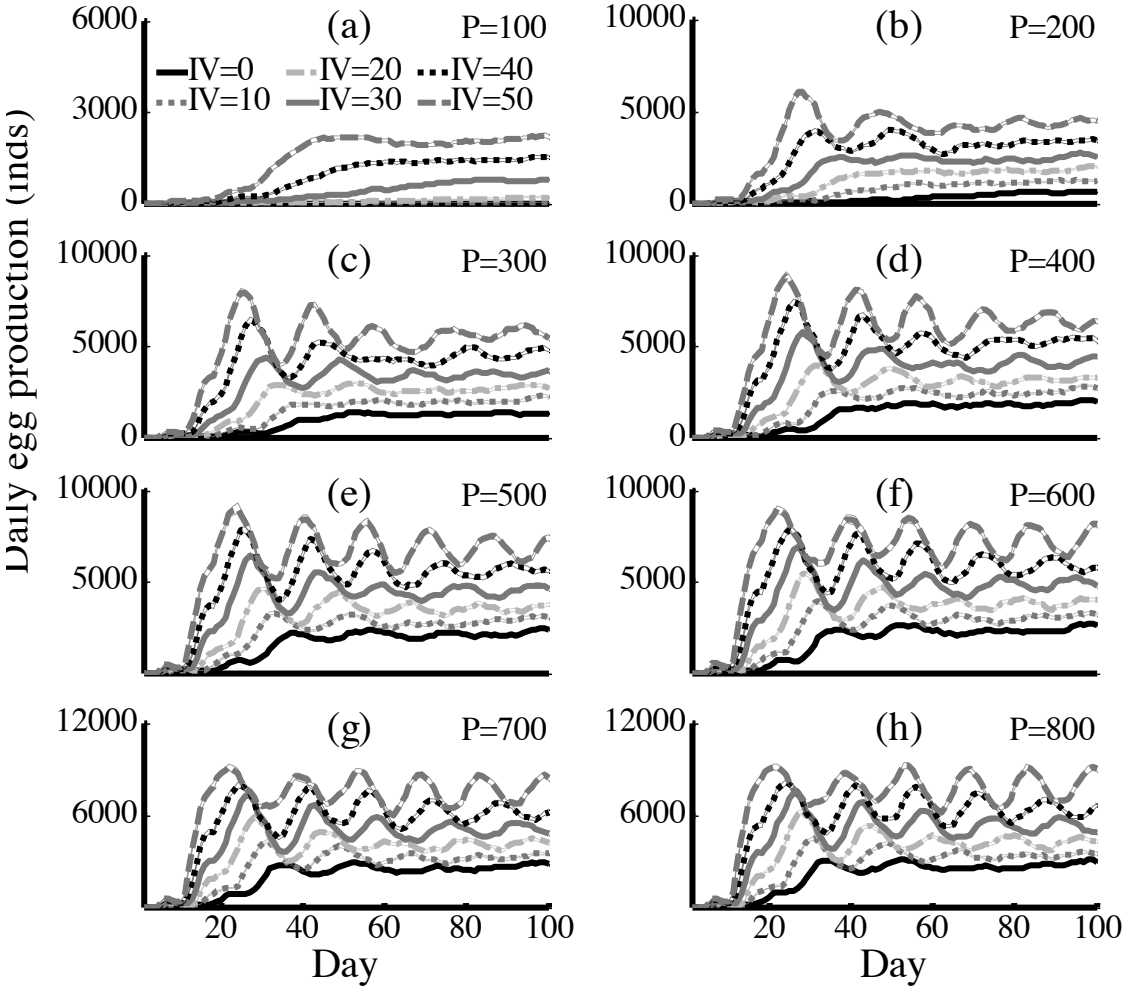

Figure 10. Experiment 2: mean daily egg production over 100 simulations for different degrees of IV under different food concentration levels. The thinner lines showed the 95% confidential intervals. All simulations were performed under favorable temperature (24 ºC) and favorable salinity (35).

3.3 Experiment 3: Individual variability and salinity

In addition to temperature and food concentration, population abundance ($F_{7, 4752}$ = 3417.92, $p < 0.01$, Figure 11a) and egg production ($F_{7, 4752}$ = 15348.65, $p < 0.01$, Figure 11b) of *A. tonsa* were significantly affected by salinity. Salinity influenced hatching rate (Figure 12), with a nonlinear relationship indicating that hatching success declined markedly with decreasing salinity after a threshold of 15.

Abundance was significantly influenced by IV ($F_{5, 4752}$ = 545.47, $p < 0.01$) in different degrees under different salinities ($F_{35, 4752}$ = 35.54, $p < 0.01$, Figure 11a). At low salinities, abundance increased with increasing IV. Using salinity of 0 as an extreme example, 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 clear increase in abundance with increasing IV. For example, when salinity was 20, 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 levels of salinity, egg production increased with increasing IV, and the relative increases were greater at low salinities (Figure 11b). Specially, when salinity was zero, mean egg production under IV = 50% was about 5 times greater than that under IV = 0 (73827.92 at IV = 0 to 398707.70 at IV = 50%); when salinity was 5, mean egg production increased about 4 times from IV = 0 to 50% (132467.60 at IV = 0 to 534971.30 at IV = 50%); when salinity was 10, mean egg production increased ~3 times

from IV = 0 to 50% (187942.50 at IV = 0 to 6 650855.40 at IV = 50%). As salinity increased, the increase in mean egg production from IV = 0 to 50% decreased further.

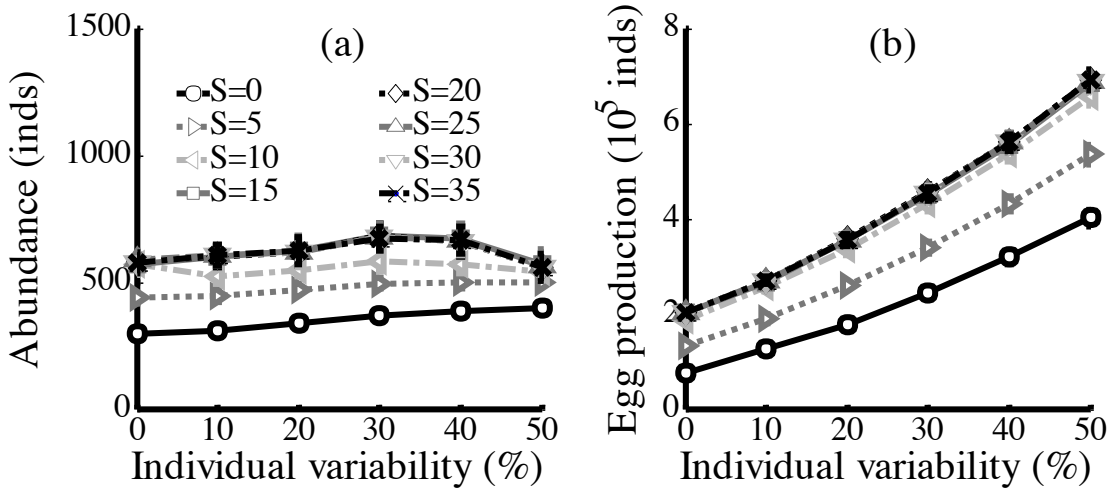

Figure 11. Experiment 3: (a) mean abundance and (b) mean egg production over 100 simulations for different degrees of IV under different salinity levels. Each error bar represented the standard error over the corresponding 100 simulations. All simulations were performed under favorable temperature (24 ºC) and favorable food concentration (800 µgC L^{-1}).

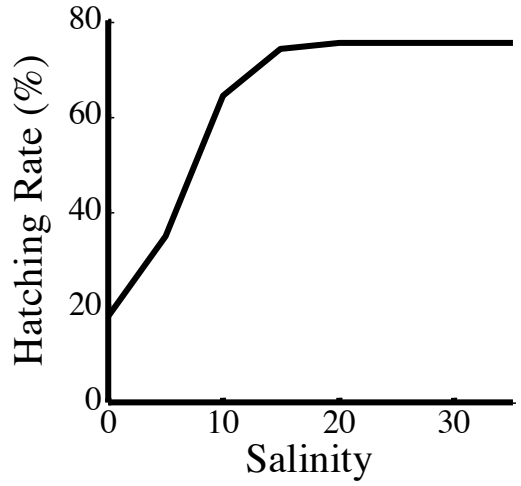

Figure 12. Expt3: a typical simulation showing hatching rate under different salinity levels. Simulation was performed under favorable temperature (24 ºC) and favorable food concentration (800 µgC L^{-1}).

Individuals with greater I_{max} and α, and smaller β_1 and β_2 were preferred (Figure 13a-d). For example, at salinity = 0, the average I_{max} value of survivors increased 26% from IV = 0 to 50 % (1.21 at IV = 0 to 1.52 at IV = 50%, Figure 13a); the average α value increased 25% (0.0068 at IV = 0 to 0.0085 at IV =50%, Figure 13b); the average β_1 and β_2 values decreased 26% (0.13 at IV = 10% to 0.10 at IV = 50%, Figure 13c,d). The selected individuals owned greater growth rates to earlier maturation (Figure 13e), so population had larger proportion of adults (Figure 13f) and higher daily egg production (Figure 14a-f). At all salinity levels, even the lowest level, populations could survive, but total abundance and egg production were subjected to salinity levels.

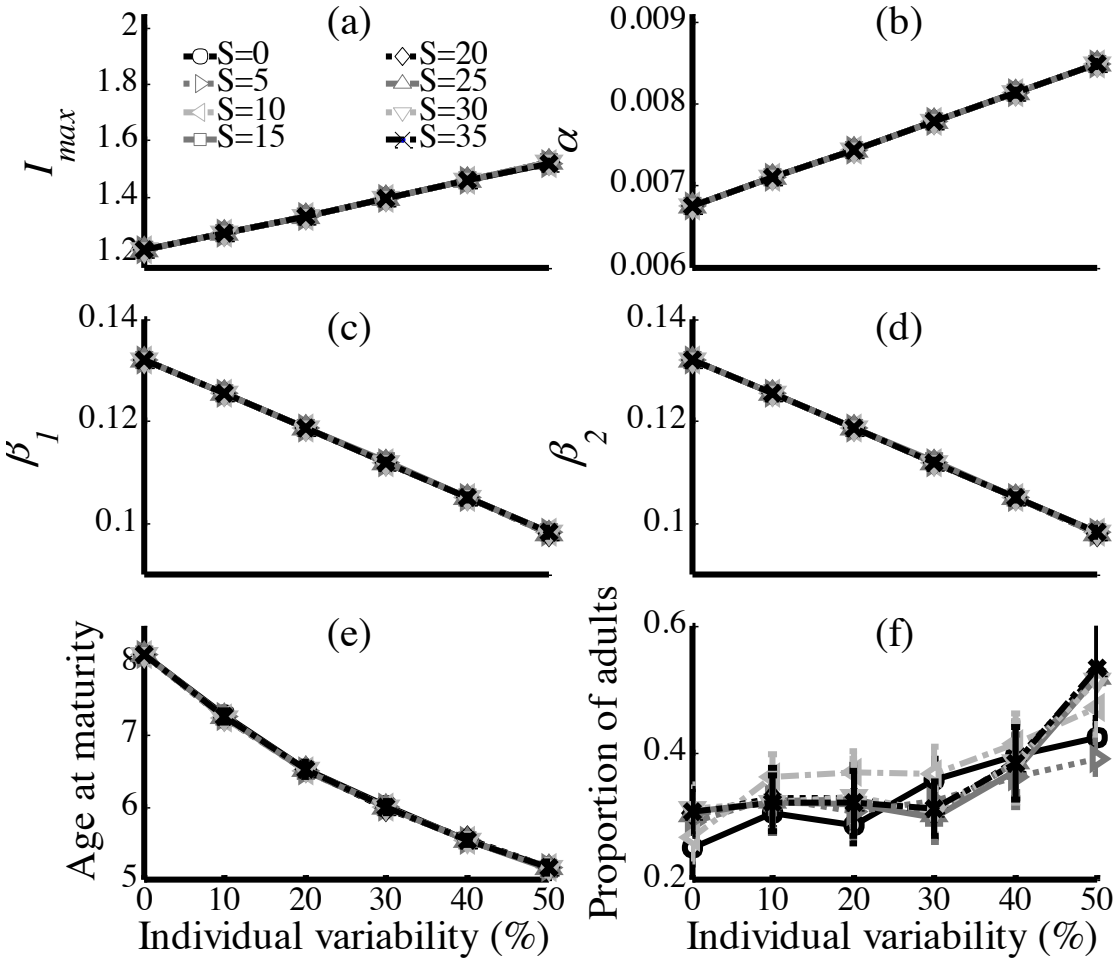

Figure 13. Experiment 3: (a-d) mean traits of survivors of the original individuals over 100 days, (e) mean age at maturity of the original individuals, and (f) mean proportion of adults over 100 days over 100 simulations for different degrees of IV under different salinity levels. Each error bar represented the standard error over the corresponding 100 simulations. See Table 1 for the definition of the four traits. All simulations were performed under favorable temperature (24 ºC) and favorable food concentration (800 µgC L^{-1}).

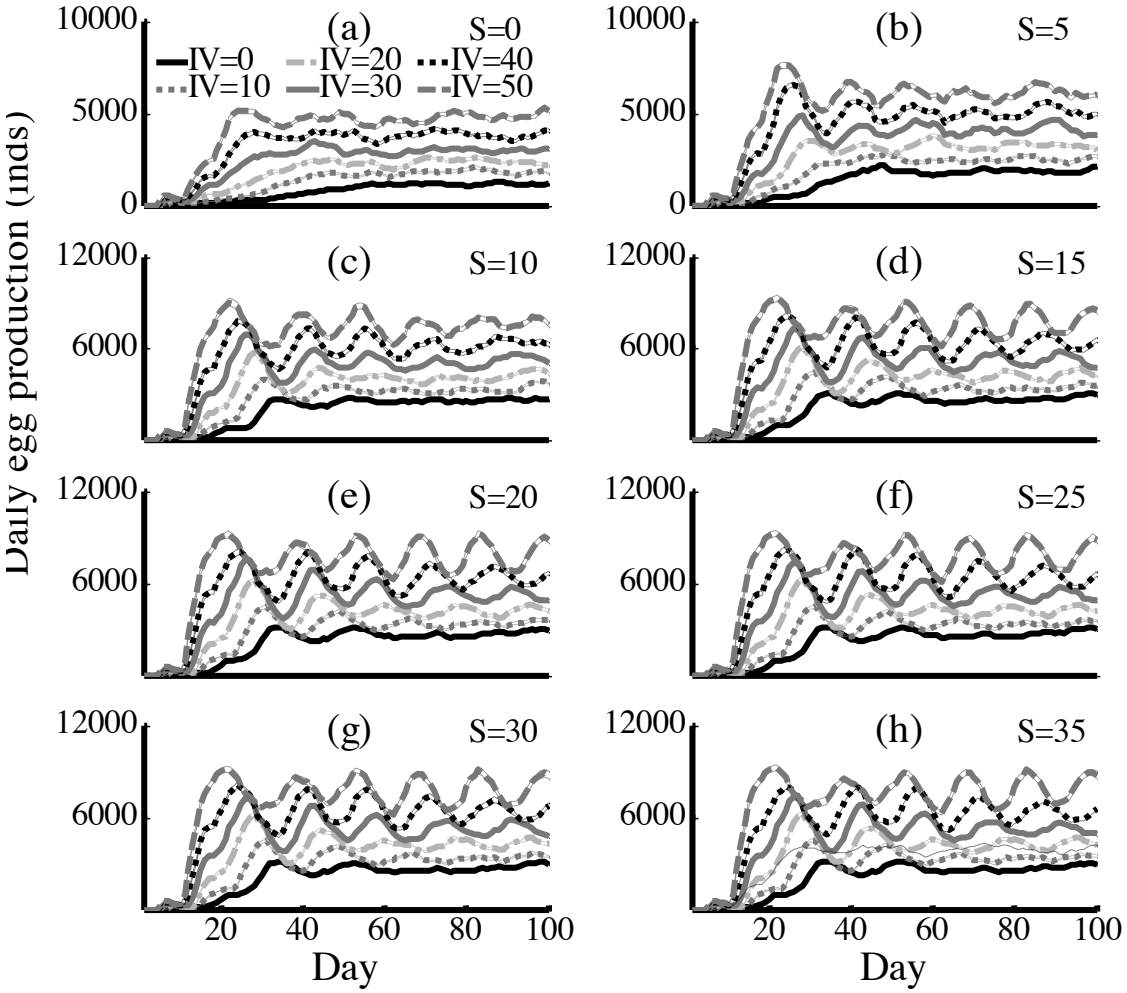

Figure 14. Experiment 3: mean daily egg production over 100 simulations for different degrees of IV under different salinity levels. The thinner lines showed the 95% confidential intervals. All simulations were performed under favorable temperature (24 ºC) and favorable food concentration (800 µgC L^{-1}).

3.4 Experiment 4: Compare effects of temperature, food concentration, salinity and individual variability on population dynamics

From Experiment 1, temperature appeared to influence population abundance in a quadratic format, so a term of central temperature (temperature minus 22) and a term of square of central temperature were added to replace the original temperature in the regression model. All terms were highly significant (Table 4). Central temperature and the square of central temperature had greater standardized partial regression coefficients, while standardized partial regression coefficient of salinity was least.

Table 4. Standardized partial regression coefficients and p-values of independent variables in the polynomial regression model.

Variables	**C.T***	**C.T^2***	**P***	**S***	**IV***
Coefficients	2.45	-2.19	0.29	0.14	0.25
P-values	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01

* C.T = central temperature that was calculated by (temperature – 22). C.T^2 = the square of C.T, P = food concentration, S = salinity, IV = individual variability.

4. DISCUSSION AND CONCLUSION

4.1 The impacts of individual variability

Life history traits relating to growth and reproduction often vary greatly among species and populations as well as individuals within a population (Ergon et al. 2001). Individuals within a population may respond to the environment in its 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). The simulation experiments demonstrated that IV benefits populations when experiencing unpredictable environmental conditions, and offers a basis for selection to operate. In the simulations, higher IV can benefit population by increasing the proportion of more adaptive individuals and ensuring population survival under various environmental conditions including different temperature, food concentration and salinity.

The simulations consistently show that under favorable environmental conditions such as optimal temperature, high food concentration and salinity, higher levels of IV can increase population performance, indicated by increasing abundance as well as egg production (see Figure 2, Figure 7, Figure 11). IV increases abundance and egg production through changing the four physiological parameters, I_{max}, α, β_1 and β_2. Under favorable temperature, food concentration or salinity, the proportion of individuals with greater I_{max} and α, but lower β_1 and β_2 increases with increasing IV. These individuals presumably grow faster and mature earlier, resulting in large proportion of adults and

high daily egg production, which potentially increases overall egg production and population abundance.

Although there is an increase on abundance and reproduction with increasing IV under favorable environmental conditions, the increase is not substantial. When environmental conditions are optimal, nearly all individuals can adapt to the environment, so the strength of environmental selection is weaker, which may lessen the effects of IV on population persistence. When there is no IV in the population, population can still sustain, which is indicated by non-zero abundance in the simulations. IV on morphological characteristics and life history traits has been discussed as an effective insurance against stressful or changing environmental conditions (Kendall & Fox 2002, Nussey et al. 2007, Schindler et al. 2010). In contrast, populations may be successful under optimal conditions without high levels of IV only if the 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 ability of environmental selection to adjust a trait of an individual becomes increasingly important as the magnitude of environmental stresses is increasing; that is, the environment becomes more unfavorable. For example, in the simulations, assuming all *A. tonsa* individuals at optimal temperature with the same growth rate, and growth rate tends to decline with decreasing temperature, for individuals with higher I_{max} and α, but lower β_1 and β_2, the relative reduction in growth rate are less, and these faster growers can pass the vulnerable early stages quickly, so

they are more likely to be selected. At lower temperature, the requirements on more adaptive individuals become even more demanding, so the strength of selection tends to be evident.

Across different levels of the three environmental factors, when they are unfavorable, higher levels of IV can increase population survival (see Figure 2a, Figure 7a, Figure 11a). In general, unfavorable conditions impose a greater challenge for population, therefore selection on individuals with adaptive traits represented as greater I_{max} and α, but lower β_1 and β_2 is stronger. The existence of more adaptive individuals, i.e., higher levels of 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, Uchmański 1999). Under stressful conditions, for populations with high IV, at least a part of individuals tend to survive, which enables populations resisting environmental stresses and even rebounding in some cases; in contrast, when there is no IV all individuals has moderate plasticity, no one can survive so that the population will experience rapid collapse (Hanski 1999, Bown et al. 2007, Reed et al. 2007, also see Figure 2a, Figure 7a, Figure 11a). Higher levels of IV in the IBM may magnify the variations in individual responses to environmental selection, potentially counteracting 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 the copepod *A. tonsa*, the effects of IV could rapidly translate into meaningful differences in population dynamics, including population persistence and population density etc.

4.2 Environmental influence

Except the significant impacts of IV on population dynamics, stochasticity in environmental factors also plays a major role in regulating the population size (Coulson et al. 2001), and is considered as a main cause for population extinction (McLaughlin et al. 2002). A considerable range in feeding, growth, egg production etc. has been reported for *A. tonsa* in relation to temperature, food concentration and salinity. For example, *A. tonsa* was found relying on constant food availability and being sensitive to small scales of patchiness (Dagg 1997); ingestion rates of *A. tonsa* increased with temperature and food availability (Kleppel 1992); egg production rates were correlated with temperature, salinity and food quality (Ambler 1986); the highest daily egg production was observed around 22 ~ 23 ºC when other environmental factors were constant (Holste & Peck 2006).

The simulation experiments demonstrated the notable effects of temperature, food concentration and salinity on life history of *A. tonsa*, which are consistent with empirical studies (e.g. Dagg 1977, Kiørboe et al. 1985, Cervetto et al. 1999). Individual life history traits vary with a changing environmental factor in the simulations. Within the range of physiological tolerance, individuals can adjust life history traits in response to environmental changes to get higher survival, which is often called as phenotypic plasticity (Pigliucci 2001). Organisms occupying variable niches display a high degree of adaptability to survive in diversified conditions via a mechanism of plasticity (Caswell 1983). Phenotypic plasticity has been widely observed in aquatic taxa including zooplankton (Black & Slobodkin 1987, Thompson 1991, Stibor & Navarra

2000). For example, copepods, such as *Calanus finmarchicus*, *Acartia hudsonica*, tend to diapause or dormancy during harsh seasons or when experiencing unfavorable conditions (Fiksen 2000, Avery 2005); some cladoceras can adjust their body lengths depending on the presence of predator (Kappes & Sinsch 2002). In the simulation, the faster growth induced by high temperature likely adjust individual body weights and presumably allow *A. tonsa* to mature quickly and decrease mortality.

However, thresholds exist for plasticity (DeWitt et al. 1998) and once exceeded, the only mechanism to sustain populations is genetic evolution or demographic rescue from neighboring persisted populations (Reed et al. 2011). This is the possible cause why *A. tonsa* tends to be absent in other ecological niches in the simulations, such as under extreme high temperature > 32 ºC, even with a high level of IV. Similar phenomenon was observed in the field. For instance, *A. tonsa* was found disappeared in Narragansett Bay, Rhode Island, for about three months, from February to April (Martin 1968), due to the death of egg caused by the freezing period (Vernberg & Vernberg 2013).

One interesting finding of the simulations is that individuals could respond to different environmental factors in varying degrees, implying individuals display diverse degrees of phenotypic plasticity under different environmental conditions and resulting in different population responses. Based on the magnitude of plasticity under each environmental factor, we can identify the most influential environmental factor. For instance, *A. tonsa* showed a greater degree of plasticity under different levels of temperature by comparing the plasticity of growth rates (Figure 3a, 8a) and egg

production rates (Figure 2b, 7b) across the temperature range and food concentration range. The finding that temperature is the most significant environmental factor is consistent with previous field observations and incubation experiments (Ambler 1985, Kleppel 1992).

4.3 Local relevance and further points

The environmental conditions in Galveston Bay are affected largely by climate change, large scale ocean variability such as sea level rise, subsidence, changes in precipitation and anthropogenic effects including overfishing and eutrophication (Warner & Tissot 2012). At annual scales, a large variation in hydrographic conditions exists in Galveston Bay. Certain combinations of the three environmental factors included in the simulations can be considered occurring seasonally at specific locations in the Bay. Therefore, the findings of the simulations potentially have local relevance to the Bay. In spring, the optimal temperature and high food concentration provide the most favorable condition for *A. tonsa* population, resulting in a predictable abundance peak. The extreme high temperature and decreasing phytoplankton biomass during summer could negatively influence population dynamics of the species; however, as temperature drops in fall, population abundance increases again to a second annual peak, and finally declines in frigid winter. The simulated two-peak annual pattern is comparable with field observations in Galveston Bay (Liu unpublished). At spatial scales, the high salinity in lower bay benefits the population, which is confirmed by pervious observations that the abundance of *A. tonsa* appeared to be higher in the more saline portions of estuaries closer to the Gulf than in the upper fresher areas (Longley 2009).

Given insufficient field research in Galveston Bay, most physiological parameters in the IBM were taken from literature (Richmond et al. 2013) whose focus was Chesapeake Bay. Therefore, the annual pattern of *A. tonsa* in Chesapeake Bay can be taken as a reference. Mean monthly abundance of *A. tonsa* in the upper Chesapeake Bay from 16 year time-series dataset (1985-2000) showed a seasonal cycle (Kimmel & Roman 2004). *A. tonsa* abundance was low in spring and increased during summer. There was only one annual peak happening from July to September. Water temperature in Chesapeake Bay changes with season, warmer in summer (~ 24 ºC) and cooler in winter (~ 5 ºC) (NOAA National Ocean Service Station). Summer water temperature in Chesapeake Bay is similar with that of Galveston Bay in spring and fall, so the two-peak annual pattern of *A. tonsa* observed in Galveston Bay corroborates the simulation findings that temperature is the most influential factor on the population dynamics of the species.

At decadal scales, hydrographic conditions in Galveston Bay show great changes. During the past 50 years, summer sea surface temperature has exhibited a gradual rise that is consistent with globally warming since the 1970s (Lester & Gonzalez 2003). The Bay has also increased in volumes due to natural and anthropogenic subsidence, as well as sea level rise (Lester & Gonzalez 2003). These changes could profoundly alter hydrographic conditions in the Bay, which could severely alter the direction and strength of selection on biotic populations, and affect the life history of marine organisms. Based on the findings of the simulations, to survive in increasing temperature, a higher level of IV under which more individuals may possess adaptive

traits is needed. When temperature increases beyond the range of tolerance, *A. tonsa* might even diapause to pass the hot summer (Fiksen 2000, Avery 2005).

I note that the current IBM to examine IV and its relevance to population dynamics was developed only focusing non-genetic effects. However, given previous studies, IV can be further divided into genetic (Scheiner & Lyman 1989, Lynch & Walsh 1998) and non-genetic components (Brock et al. 2009, Reed et al. 2010). Genetic variations among individuals within a population should not be ignored as this will determine its evolutionary potential (Scheiner & Lyman 1989). More attention on genetic effects is needed for future research.

In conclusion, findings of this study show that the effects of environment changes on population dynamics are modulated by IV. Individuals can adjust their life-history traits to the environments encountered to some extent, and more adaptive individuals tend to be selected. Given a changing environment subjected to natural and anthropogenic stressors, incorporating IV into research on population dynamics will improve our ability to understand mechanisms of regulating population dynamics in response to environmental changes and population evolution.

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