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Individual variability and environmental conditions: effects on zooplankton cohort dynamics

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ABSTRACT: We use an individual-based cohort model of the planktonic calanoid copepod *Acartia tonsa* to examine how variability among individuals in bioenergetic traits affects cohort dynamics. The model follows a cohort of individual zooplankton through the hourly processes of feeding and energy distribution among growth, development, and reproduction, under high and low rates of size-dependent mortality. The degree of variability in traits among individuals was quantified by the coefficient of variation (CV). In our first simulation experiment (Expt 1), population growth rate (λ) increased with increasing variability among individuals (increasing CV) when overall mortality was high; egg production increased with CV under high and low mortality rates, and survival was unaffected by the degree of trait variability. Expt 2 tested the effect of genetic makeup on cohort dynamics; when mortality rate was high, increasing CV resulted in individuals with correlated traits having higher egg production and λ than individuals with randomly assigned traits. Expt 3 tested how environmental conditions altered the effect of CV on survival, egg production, and λ. Population growth rate increased with increasing CV under high mortality rate and suboptimal conditions. Our analyses demonstrate how small differences in the values of individual-level traits can influence growth and reproduction which can in turn translate into ecologically important effects on cohort dynamics. The effect of increased variability among individuals on cohort dynamics was particularly important when environmental conditions were poor, when the mortality rate was high, and under certain types of size-dependent mortality. These results may have important implications for understanding the dynamics of populations experiencing stress.

KEY WORDS: Variability among individuals · Fitness · Cohort dynamics · Individual-based model · *Acartia tonsa* · Environmental conditions · Size-dependent mortality

INTRODUCTION

Many abiotic and biotic factors have been shown to influence population and community dynamics. Abiotic factors include temperature, nutrient levels, and habitat quantity, quality, and spatial arrangement (e.g. Andrewartha & Birch 1954, Richardson & Schoeman 2004, Harley et al. 2006). Common biotic factors affecting population dynamics include predation, competition, and the behavioral, morphological, physiological, and life-history traits of individuals (Begon et al. 1986, Stearns 1992, Roff 2002). Individuals within the same population often differ in their responses to environmental and biological conditions. These differences can influence the survival, growth, and reproductive success of individuals, which can in turn influence population dynamics (Łomnicki 1988, Koehl 1989, Clark 2003).

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Individual-level traits likely to be important in population dynamics are those that result in significant differences in an individual's relative fitness. Examples include behavioral responses to predation risk that affect survival and growth, with potentially subsequent effects on fecundity (e.g. Skelly & Werner 1990, Anholt & Werner 1995, Fryxell & Lundberg 1998), body size, which affects reproductive output and mortality risk (e.g. Brooks & Dodson 1965, Blanckenhorn 2000), and bioenergetic traits related to foraging and growth rate efficiency (e.g. Schoener 1971). Bioenergetic traits may be particularly important for taxa with high mortality of young and size-dependent reproduction. Rapid growth rates during the high-mortality early life stages can lead to dramatic increases in survival, younger age at maturity, and larger adults capable of producing more offspring (Roff 2002).

We might expect that populations comprised of individuals with a high degree of variability in bioenergetic traits would be more resilient and resistant to changes in environmental conditions. Variability among individuals may increase the probability that at least some individuals in the population will be well equipped under a wide range of environmental conditions. This could occur either if there are individuals that do well across multiple conditions, or if the composition of traits in the population changes as conditions change, such that different individuals dominate under each set of conditions. This is the population-level analog to species complementarity, in which the particular species dominating a system changes with conditions, while system function is maintained by at least some species under all (or most) conditions (Wallace 1977, 1982, Schindler et al. 2010). Variability in traits among individuals may be particularly important for populations experiencing unfavorable or stressful environmental conditions, potentially augmenting population persistence and stability and affecting population growth rates (Bjørnstad & Hansen 1994, Brunkow & Collins 1996, Hanski & Saccheri 2006). It has been proposed that populations under environmental stress show a greater degree of individual-level variability (Warwick & Clarke 1993, Bubliy et al. 2000, Pfister & Stevens 2002).

Concomitant with increased recognition of the links between individual variability and population dynamics has been the rise of individual-based modeling (DeAngelis & Mooij 2005, Neuheimer et al. 2010). Historically, population modeling focused on directly predicting aggregate quantities such as total number of individuals (e.g. Łomnicki 1992), in which models were constructed without considering that individuals in the population can differ significantly in traits that have ecologically meaningful repercussions. Structured approaches originally divided the population into age- or stage-classes (Caswell 2001), allowing the vital rates to differ among classes but not explicitly among individuals within a class. More recently, the structured approach has been extended by modeling the population as the sum of its component individuals. Individual-based modeling permits each individual to have a unique set of traits; these models have yielded realistic population and community-level predictions, while allowing examination of the individual-level processes and traits responsible for the higher-level dynamics (Grimm & Uchmanski 2002, DeAngelis & Mooij 2005, Breckling et al. 2006). One of the strengths of the individual-based approach is that it allows the determination of which individual-level traits contribute disproportionately to cohort and population dynamics.

We constructed an individual-based model of *Acartia tonsa* to evaluate the hypothesis that the degree of variability in key bioenergetic traits among individuals influences cohort survival, reproductive success, and population growth rate. *A. tonsa* is an ubiquitous and abundant planktonic copepod (Heinle 1966, Mauchline 1998), comprising up to 95% of the estuarine summer zooplankton assemblage in the eastern United States and inhabiting regions with a wide range of environmental conditions (Jeffries 1962, Heinle 1969, Tester 1985). *A. tonsa* is an important food source for gelatinous zooplankton and for many species of planktivorous fishes. We simulated growth, survival, and egg production of a cohort over 40 days. We assigned values of bioenergetic traits to individuals randomly and in a correlated manner, and explored cohort dynamics under favorable (fast growth) and unfavorable (slow growth) environmental conditions using size-independent mortality and several alternative size-dependent mortality functions. The alternative mortality functions represent different types of predators. We report on the results of 3 simulation experiments. Expt 1 examined effects of individual variability on cohort dynamics under both size-independent and size-dependent mortality rates, with favorable environmental conditions and randomly assigned bioenergetic traits. We then evaluated whether the results of Expt 1 were robust when bioenergetic traits were assigned to individuals in a correlated fashion (Expt 2), or under less than favorable environmental conditions (Expt 3).

METHODS

Model description

Overview

The model followed a cohort of individual zooplankton through the daily processes of growth, development, mortality, and reproduction using a one hour time step. All individuals started on the same day, as first-stage nauplii. Growth in weight of each individual was based on bioenergetics, with ingestion dependent upon food availability (phytoplankton concentration) and body weight. Daily mortality of individuals was represented as constant or as depending on body length. Once mature, daily egg production was computed based on net energy available from food consumption. All model equations were difference equations solved iteratively with a one hour time step; all reported parameter values were used to compute daily rates each hour, which were then divided by 24 to update body weight, egg production, and survival.

Assimilated carbon from food was partitioned between a body pool and a molt (exoskeleton) pool. Metabolic losses were assumed proportional to each of the body and molt carbon pools. When molt carbon (S; µg C) exceeded a threshold (S_T; µg C), the individual molted into the next life stage and body length was updated. A total of 12 life stages (6 naupliar, 5 copepodite, and 1 adult stage) were represented; thus there were 11 values of S_T. All assimilated carbon beyond metabolism for individuals in the adult stage went to egg production. Mortality rate was specified as either a constant (size-independent mortality) or as one of 3 differently-shaped functions of body length. Mortality rate was converted to the probability of dying, and each individual was evaluated daily. The growth and development components of the model were modified from van den Bosch & Gabriel (1994).

Growth and development

Two state variables related to an individual's weight were followed: body carbon and molt (exoskeleton) carbon. Daily growth of body carbon (W; µg C) and molt carbon were the differences between assimilated carbon and the carbon lost to metabolism:

$$\Delta W = (\kappa \times A) - M_1 \quad (1)$$

$$\Delta S = [(1 - \kappa) \times A] - M_2 \quad (2)$$

where κ represents the fraction of assimilated carbon that goes to body carbon, A is assimilated carbon (µg C d^{-1}), and M_1 and M_2 are metabolic losses (µg C d^{-1}) associated with the maintenance of body and the building of a new molt (exoskeleton), respectively. κ was set to 0.866 (Table 1) based on calibration (see 'Parameter estimation').

Individuals could not lose weight (carbon); if metabolic costs exceeded assimilated carbon, then ΔW and ΔS were set to 0. While real copepods in natural conditions can lose weight, the model was designed for simulating weight gain, and predicts unrealistic weight loss under starvation conditions. Because our simulations did not involve phytoplankton concentrations at or below maintenance levels, the model predicts realistic growth under all simulated conditions. The assimilated carbon each day was based on

Table 1. Variable and parameter names, description, units, and values used in the individual-based copepod cohort model. The model was modified from van den Bosch & Gabriel (1994); some parameter values were changed to configure the model for *Acartia tonsa*. For the 4 simulated time-dependent variables (W, S, L, and A), mean initial values are shown (for newly hatched individuals), and the range of mean values are shown, in parentheses, for adults in simulations across results for coefficient of variation (CV) = 0 to 50%. Values for β_1 and β_2 were specified prior to calibration based on van den Bosch & Gabriel (1994). The mean values for I_{max}, α, θ, and γ were determined by calibration. The value of κ was then set after calibration to obtain realistic molting dynamics. The phytoplankton growth rate (r) was only used for density-dependent simulations reported in the 'Discussion'

Variable	Description	Units	Value
W	Carbon content of body	µg C	0.2 (6.3–8.0)
S	Carbon content of molt (exoskeleton)	µg C	0.001
L	Length of individual	mm	0.22 (1.2–1.3)
A	Carbon assimilation rate	µg C d^{-1}	0.2 (3.9–6.8)
β_1	Metabolic costs for maintenance as a fraction of the body carbon pool	d^{-1}	0.132
β_2	Metabolic costs of molting as a fraction of the molt carbon pool	d^{-1}	0.132
I_{max}	Maximum ingestion rate	µg C (µg C copepod)$^{-1}$ d^{-1}	1.209
α	Shape parameter of the functional response	(µg C)$^{-1}$	0.00675
θ	Shape parameter relating maximum ingestion to weight		0.850
γ	Carbon assimilation efficiency	fraction	0.504
κ	Fraction of assimilated carbon (A) accumulated as body carbon	fraction	0.866
x	Phytoplankton concentration	µg C l^{-1}	500 or 1000
r	Phytoplankton growth rate	d^{-1}	0.8

ingestion rate and assimilation efficiency. A was a function of food (phytoplankton) concentration and body weight:

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

where I_{max} is the maximum ingestion rate of an individual per unit volume [µg C ingested (µg C copepod)$^{-1}$ d^{-1}], α is the shape parameter of the functional response relationship (µg C)$^{-1}$, θ is the shape parameter for the effect of body size on maximum ingestion, x is the food concentration (µg C l^{-1}), and γ is the assimilation efficiency. A is therefore in units of µg C copepod^{-1} d^{-1}.

Basal or 'standard' metabolism was computed as proportional to each of the body (M_1) and molt (M_2) carbon pools:

$$M_1 = \beta_1 \times W \quad (4)$$

$$M_2 = \beta_2 \times S \quad (5)$$

where β_1 and β_2 are metabolic costs as a fraction of the body and molt carbon pools. Both β_1 and β_2 were set to 0.132 (Table 1). M_1 and M_2 reduce the amount of assimilated carbon available for growth and reproduction. While other studies and models have used a similar simple weight-dependent relationship (e.g. Cervetto et al. 1993, Ikeda et al. 2001, Batchelder et al. 2002, Gentleman et al. 2008), metabolic rate has also, in some cases, been expressed as dependent on ingestion (e.g. Kiørboe et al. 1985, Båmstedt 1988, Thor et al. 2002). Metabolic rates, generated using our simple equation and adjusted for temperature, yielded values comparable to those measured for *Acartia tonsa* (Table 2, metabolic rate).

Molting and advancement to the next stage occurred when the amount of molt carbon exceeded a threshold value (see 'Parameter estimation' below). Upon molting, molt carbon was reset to zero. This process of feeding, assimilation, buildup of carbon for the next molt (building of a new exoskeleton), and molting was repeated until the individual reached the adult stage. Length (L) was computed at each molt using a length–weight relationship [$L = \ln(8.45) - \ln(4.45 - \ln W)$] and the weight on the day of molting. Length remained at that value until the next molting (Table 1).

Table 2. Simulated (present study) and reported metabolic rates and growth efficiencies for calanoid copepods. Metabolic rates are shown as % of body carbon per day. Published metabolic rates are reported as respiration and converted into carbon losses if not already in units of carbon. Model predictions of metabolic rate were calculated as the proportion of the body carbon (W) pool lost to metabolism each day (β_1) (see Table 1), and were adjusted for temperature using a Q_{10} of 2.0. Simulated and reported growth efficiency values (K_1) are the percentage of ingested carbon that is converted into body carbon each day. Subscripted comments provide explanation of any calculations necessary to convert published values into the units reported here

Metabolic rate

Species	Value (% body C d^{-1})	Conditions and life stages	Source
Acartia tonsa	8.7–20.0	12–24°C, 500–1000 µg C l^{-1} phytoplankton, all life stages	Present study
Acartia tonsa	17–18[a]	18°C, 916 µg C l^{-1} phytoplankton, adult females used	Kiørboe et al. (1985)
Acartia tonsa	15.5–41[a,e]	20°C, 0–500 µg C l^{-1} phytoplankton, field-collected adults used	Thor et al. (2002)
Acartia tonsa	18.4[a]	22°C, field-collected individuals	Ikeda et al. (2001)
Acartia australis	14.1	24.5°C, field-collected individuals	Ikeda & Skjoldal (1980)
Calanus pacificus	13.3–28.2	12–16°C, all life stages	Vidal 1980

Growth efficiency

Species	Value (%)	Conditions and life stages	Source
Acartia tonsa	25–40	12–24°C, 500–1000 µg C l^{-1} phytoplankton, all life stages	Present study
Acartia tonsa	44[b]	16–18°C, unlimited phytoplankton, nauplii and copepodites only	Berggreen et al. (1988)
Acartia tonsa	10–55[c]	20°C, adult females	Roman (1977)
Acartia tonsa	39[d]	18°C, 916 µg C l^{-1} phytoplankton, adult females used	Kiørboe et al. (1985)
Acartia hudsonica	19–40[d]	4.5–16°C, ≤ 590 µg C l^{-1}, field-collected adult females used	Durbin & Durbin (1992)

[a]Converted using the equation 1 ml O_2 = 0.43 mg C, and the estimated C content of *Acartia tonsa* as approximately 45% of dry weight (data and conversions from Ambler 1985, Kiørboe et al. 1985); [b]Calculation done after metabolic losses were subtracted from ingestion; [c]Copepods feeding on one species of phytoplankton and on detritus found on *Fucus vesiculosus*; [d]Gross growth efficiency calculated using or including egg production/ingestion (i.e. compared to only using biomass production for immature stages); [e]Respiration changed with diet

Reproduction

Upon reaching the adult stage, all assimilated energy in excess of metabolism was devoted to egg production. Each hour, egg production by each adult female was computed as the amount of assimilated carbon not metabolized, divided by an average weight of an egg. We use an average weight of 0.035 µg C egg^{-1} based on reported values for *Acartia tonsa* (Ambler 1985, Kiørboe et al. 1985, Durbin et al. 1992). On the last hour of each day, daily cohort egg production was computed as the sum across the hourly values for each adult female individual, and then over all adult females. Egg production was treated as a prediction variable and used in calculations of population growth rate (λ; d^{-1}); the fate of produced eggs was not followed in model simulations. We present 2 output variables related to cohort egg production: daily cohort egg production (summed over hours and individuals for each day) and total cohort egg production (cumulative number of eggs produced by the cohort over the 40 d simulation).

Mortality

Each individual copepod was evaluated hourly for whether it survived or died. Four different mortality curves were used: size-independent mortality, and 3 curves dependent upon zooplankton length (Fig. 1). On each day, the effective mortality rate was obtained from the appropriate curve, either a constant (size-independent) rate or a rate based on the length of the individual. This instantaneous mortality rate was then converted to a probability of dying per hour. A uniform random number between 0 and 1 was generated, and if the random number was less than the probability of dying, the individual died and was removed from the simulation.

The 4 mortality curves were specified to reflect different predator fields likely experienced by copepod zooplankton. Size-independent mortality was the simplest assumption about mortality. Mortality rate increasing with zooplankton length was appropriate in simulating situations in which predation is dominated by larger invertebrate and some vertebrate predators. The medusa *Chrysaora quinquecirrha* selectively feeds on the largest individuals of *Acartia tonsa* (Purcell 1992, Suchman & Sullivan 1998), and larger larval fish and juveniles generally prefer larger zooplankton (Hunter 1981). Mortality rate decreasing with zooplankton length represented a situation in which predation is dominated by size-selective predators that preferentially feed on smaller individuals, such as the ctenophore *Mnemiopsis leidyi*, an important predator of *A. tonsa* (Deason 1982, Waggett & Costello 1999). A dome-shaped mortality curve can arise in situations in which predation is dominated by predators that specialize on intermediate-sized zooplankton, or can arise from a mixture of different types of predators. For each mortality curve, 2 levels of overall mortality rate (low and high) were determined by calibration (see 'Parameter estimation').

Parameter estimation

We first calibrated the values of I_{max}, α, θ, γ, and κ. Values for I_{max}, α, θ, and γ (not κ) were initially set to the average values suggested by van den Bosch & Gabriel (1994) for calanoid copepods. We then estimated values of these parameters using a Monte Carlo filtering method (Rose et al. 1991). We specified large CVs for these parameters and ran simulations on thousands of individuals with randomly assigned parameter values. We then selected individuals with values of these parameters that led to growth in lengths, weights, and age at maturation realistic for *Acartia tonsa*. The targets were growth under favorable conditions to mature adult (final molt) lengths between 1.0 and 1.3 mm, body weights between 6 and 8 µg C ind.$^{-1}$, and age at maturity of 7 to 10 d. The averages of these parameter values for the '*Acartia*-like' copepods were then used as the mean values in all simulations (Table 1). Our value of κ (0.866) was then determined

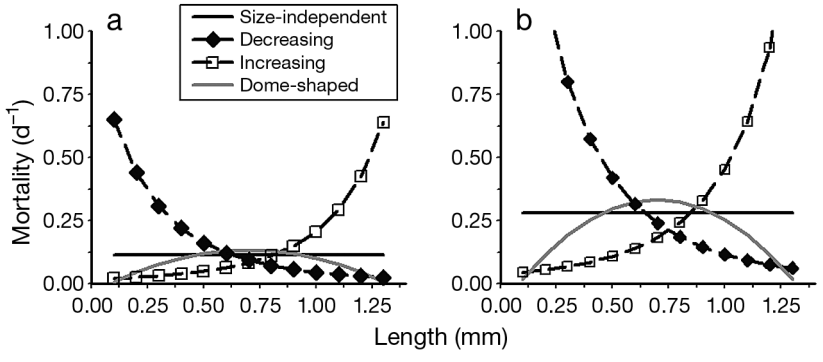

Fig. 1. Four types of mortality curves (size-independent, decreasing, dome-shaped, increasing) used in model simulations under (a) low and (b) high mortality rates. Each mortality curve relates mortality rate to individual copepod length

such that with these mean values of bioenergetics parameters, the predicted molt carbon was approximately 10% of the total body carbon (van den Bosch & Gabriel 1994).

The second step in the calibration was to determine the 11 S_T values required for molting by stage (Table A1 in Appendix 1). Thresholds were determined after many simulations as the mean molt carbon at molting when 75% of individuals in the cohort had molted, using van den Bosch & Gabriel's (1994) criterion that the molt carbon is at least 5% of the carbon in the copepod body pool.

The third and final step in the calibration was to determine the high and low mortality rates for each of the 4 alternative mortality curves (Fig. 1). We performed simulations with the parameter values and threshold weights fixed at their values and varied the mortality rates. We determined a low and high mortality for each of the 4 mortality curves such that the low mortality curve resulted in the survival to maturity of 10% of the individuals under poor abiotic environmental conditions (low temperature, low food concentration) and the high mortality condition resulted in 10% survival to maturity under favorable abiotic environmental conditions (high temperature, high food). The resulting mortality rates for the size-independent case were 0.114 d^{-1} for the low condition and 0.280 d^{-1} for the high condition. These rates were consistent with estimates of daily mortality rates for broadcast spawners like *Acartia tonsa* (e.g. Heinle 1966, Deason 1982, Purcell et al. 1994, Hirst & Kiørboe 2002).

Initial conditions for simulation experiments

Each simulation began with 10 000 first-stage naupliі individuals. Initial S was set to 0 for all individuals in all simulations. Values of initial body C (W at time = 0, W_0), I_{max}, α, and β_1 and β_2 were assigned to each individual at the beginning of each simulation. The SD for W_0 was calculated as 10% of mean W, and the minimum and maximum weights were defined as the mean $W \pm 2$ SD. Initial L (L_0) was computed from W_0 using the length–weight relationship.

I_{max}, α, and β_1 and β_2 were assigned to individuals in 1 of 2 different fashions (random or correlated) we refer to as genetic makeups. In all cases, we assigned values to individuals from normal probability distributions by defining the mean, SD, and minimum and maximum values for each of the 4 parameters (Table 1). The mean values were always the averaged value determined from calibration. We examined a range of assumed SD (or equivalently CVs, where CV = 100 × [SD/mean]) for the 4 parameters. Minimum and maximum values were always specified as the mean value ± 2 SD.

In the random genetic makeup, all 4 parameters were independently generated from 4 separate normal distributions. The assignment of values of each parameter to individuals was made without regard to the values of the other traits. The resulting initial cohort of 10 000 individuals represented the full range of possible combinations of these 4 traits.

In the correlated genetic makeup, the value of I_{max} assigned to an individual was positively correlated with α, and negatively correlated with β_1 and β_2. Higher values of α imply higher ingestion rates, such that an individual with a high value of I_{max} and a high α are efficient feeders. For each simulation, a single normal deviate (mean = 0; SD = 1) was generated and used to determine the values of all 4 traits for an individual. The value of each of the 4 traits was computed as the normal deviate times the SD for the trait plus the mean value for the trait. We used the same value of the normal deviate for I_{max} and α, and the negative value of the normal deviate for β_1 and β_2 to force a positive correlation between I_{max} and α, and a negative correlation between I_{max} and β_1 and β_2. This results in normal distributions of values for each of the traits, but with all 4 distributions being completely correlated. Model individuals thus fell along a continuum from efficient feeders with high ingestion rates and low metabolic rates at one extreme to inefficient feeders at the other extreme.

We used a Q_{10} to adjust the calibrated mean values of the parameters for cooler and warmer temperatures. All parameter values shown in Table 1 were assumed to be appropriate for 18°C because most laboratory experiments we relied on were performed at similar temperatures, and 18°C was halfway between our low (12°C) and high (24°C) temperatures used in simulations. We adjusted the values I_{max}, α, β_1, and β_2 for 12°C and 24°C assuming a Q_{10} value of 2.0 which is typical of, and perhaps conservative for, copepods (e.g. Kiørboe et al. 1982, Durbin & Durbin 1992). Mean values of parameters were multiplied by 0.66 for 12°C and by 1.51 for 24°C.

Typical simulation results

All model simulations were of 40 d duration using an hourly time step; by the last day of each simulation, less than 1% of the initial cohort survived. Typical trajectories of daily length and body carbon for

an individual are shown in Fig. 2a,c; the proportion surviving and daily cohort egg production are shown in Fig. 2b,d. Individual growth in the model approximated isochronal growth, as has been observed in *Acartia tonsa* in the field (Landry 1975, 1983, Miller et al. 1977, Klein Breteler et al. 1994). Simulated growth was not truly isochronal because molt durations did increase slightly through development (Fig. 2a).

Design of simulation experiments

Three simulation experiments were performed to test the importance of variability among individuals on survival, egg production, λ, and traits of survivors to maturity. These experiments involved using various combinations of 3 factors: size-dependence of mortality (Expt 1), genetic makeup of individuals (Expt 2), and environmental conditions (Expt 3).

Environmental conditions were defined by temperature and phytoplankton concentration. Two temperatures (12 and 24°C) and 2 phytoplankton concentrations (500 and 1000 µg C l^{-1}) were used. These temperatures and phytoplankton concentrations are representative of the range of conditions encountered by *Acartia tonsa* in estuaries along the eastern US coast (Kremer & Nixon 1977, Purcell et al. 1994), particularly in Chesapeake Bay (Heinle 1966, Olson 1987, see also Chesapeake Bay Program data at www.chesapeakebay.net) and in Narragansett Bay (Kremer & Nixon 1977). The combination of 24°C and 1000 µg C l^{-1} is considered favorable for growth and reproduction of *A. tonsa* (Conover 1956), while 12°C and 500 µg C l^{-1} were considered unfavorable, although adults are found in estuarine regions under these conditions (e.g. Heinle 1966). In nature, *A. tonsa* encounters more extreme conditions than 24°C and 1000 µg C l^{-1} (e.g. warmer water in the shallows, algal blooms); our intent was to contrast environmental conditions considered typical of Chesapeake Bay at different times of the year when *A. tonsa* is present.

The magnitude of individual variability was varied by specifying the CV of the normal distributions for initial weight and for the 4 bioenergetics traits (I_{max}, α, β_1 and β_2). We used 3 levels of CV: 0, 25, and 50%. Variability of 25% has been documented as a common (perhaps conservative) degree of variability in bioenergetic traits such as ingestion and metabolic rates in natural copepod populations (Båmstedt 1988, Durbin et al. 1990, Thompson et al. 1994). We included the CV of 50% to confirm some of the more subtle trends and patterns observed at lower values of CV.

Expt 1: Variability and size-dependent mortality

A 3 × 4 × 2 full factorial design was used with all 3 levels of individual variability as one factor, the mortality curves (size-independent mortality plus the 3 size-dependent relationships) as the second factor, and mortality level (low or high mortality rates) as the third factor. All simulations were performed using the favorable environmental conditions (24°C and 1000 µg C l^{-1}) and random genetic makeup.

Expt 2: Correlated genetic makeup

A 3 × 4 × 2 × 2 full factorial design was used in this experiment, including all 3 levels of variability among individuals, 4 types of mortality curves, 2 mortality levels (as in Expt 1), and 2 types of genetic makeup (random or correlated bioenergetic traits). Expt 2 was a repeat of Expt 1, but with correlated genetic makeup included. Thus, the results of Expt 2 for the random genetic makeup were the same as reported for Expt 1.

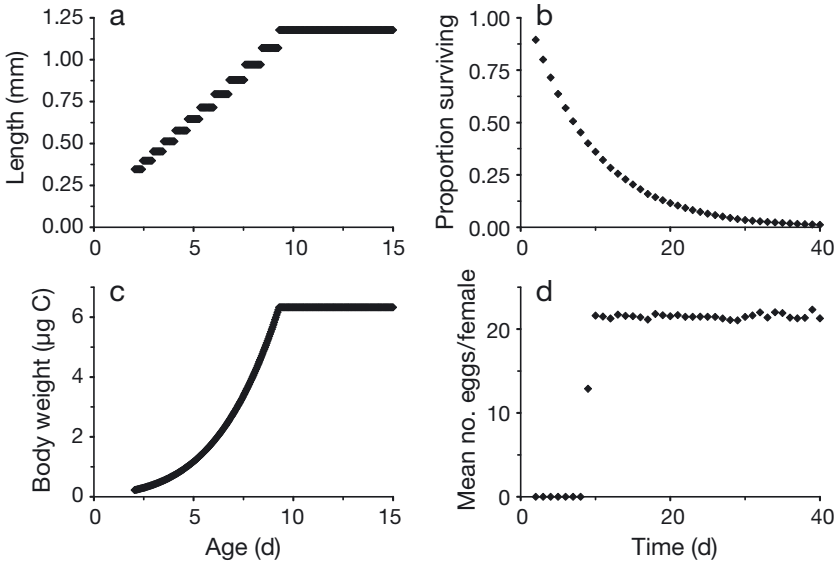

Fig. 2. Model predictions for a typical simulation showing daily values of (a) body length of an individual, (b) proportion of the original cohort surviving, (c) body carbon weight of an individual, and (d) mean daily egg production per individual. Panels (a) and (c) are for an individual copepod; panels (b) and (d) are based on a cohort that started with 10000 individuals

Expt 3: Unfavorable environmental conditions

A 3 × 2 × 2 × 2 full factorial experiment was used with the magnitude of individual variability (3 levels of CV) as one factor, mortality type (2 levels: size-independent or decreasing) as the second factor, mortality level (as in Expt 1: low or high mortality rate) as the third factor, and environmental conditions (2 levels: favorable defined as 24°C and 1000 µg C l^{-1} phytoplankton, and unfavorable defined as 12°C and 500 µg C l^{-1}) as the fourth factor. All simulations used the random genetic makeup. Expts 1 and 2 both used the favorable environmental conditions. In addition to size-independent mortality, the decreasing mortality curve was used in Expt 3 because with this mortality curve, individual variability had an effect on cohort dynamics in Expts 1 and 2, and the decreasing curve is a reasonable assumption about the size-dependence of zooplankton mortality.

Analysis of prediction variables

The model prediction variables examined for cohort dynamics were: proportion of the original cohort that survived to maturity, daily cohort egg production, and the total cohort (cumulative) egg production. We also combined the daily predictions of survival and egg production into a 12 stage pre-spawning census matrix projection model, and computed for the cohort λ from the output of the individual-based model. The use of λ is a compact way to summarize the net effects of changes in survival, growth, and reproduction, and was calculated as the dominant eigenvalue of the stage-based matrix. We used a full stage-based matrix model to estimate λ because it is an exact solution and we were interested in potentially small changes in λ across treatments in the simulation experiments. Simpler methods of calculating λ, such as those based upon net reproductive rate and generation time, are approximations (Case 2000) and can get complicated for stage-based situations (Caswell 2001).

The matrix model was estimated from model simulation predictions. The transitions in the stage-based matrix included P_i (probability of staying in the same stage, i), G_i (probability of molting into the next stage), and F_i (number of female eggs laid per female). F_i was calculated as 50% of eggs produced per female per day which survived to hatch, assuming a 50:50 sex ratio (Durbin et al. 1983). We used a conservative estimate that 50% of eggs hatch and survive to first stage nauplii (Mauchline 1998); therefore, F_i was 25% of eggs laid by females each day, after the sex ratio and egg mortality were taken into account.

P_i and G_i were calculated as follows:

$$P_i = \sigma \times (1 - \rho) \quad (6)$$

$$G_i = \sigma \times \rho \quad (7)$$

where $\sigma = e^{-z}$, z being the realized daily instantaneous mortality rate, and $\rho = \frac{\sigma^D - \sigma^{D-1}}{\sigma^D - 1}$, D being stage duration (d). Using the model outputs, we computed the average values of D and z by stage, based on all individuals that survived the stage. These values were then used to compute P and G values for a simulation, which, when combined with estimated values of F, allowed calculation of λ. Table A2 shows an example of the estimation of these transition elements for the stage-based matrix.

To understand the resulting influences of differential survival of individuals on the composition of the mature cohort, we reported the mean values of 5 traits of individuals upon reaching maturity: age, length, α, I_{max}, and β_1. The 3 model prediction variables (survival to maturity, daily cohort egg production, and total cohort egg production), their combined effects (λ), and the mean values of 5 traits of survivors to maturity were reported for Expt 1. Survival, total cohort egg production, and λ were reported for Expts 2 and 3.

Twenty replicate simulations were performed for each treatment combination in each experiment. We show only means on figures, because the variability among means of replicate simulations was small. Standard deviations among means for survival and λ were generally less than 2% of the mean value, and for total cohort egg production were less than 4% of the mean value.

RESULTS

Expt 1: size-dependent mortality

CV had little effect on survival to maturity under all of the low and high mortality rate versions of the 4 mortality curves (Fig. 3a,b). The type of mortality curve had a greater influence on survival to maturity when mortality rate was low (Fig. 3a) than when mortality rate was high (Fig. 3b). Under the low set of mortality rates, the greatest proportion of individuals survived to maturity with dome-shaped and decreasing mortality curves.

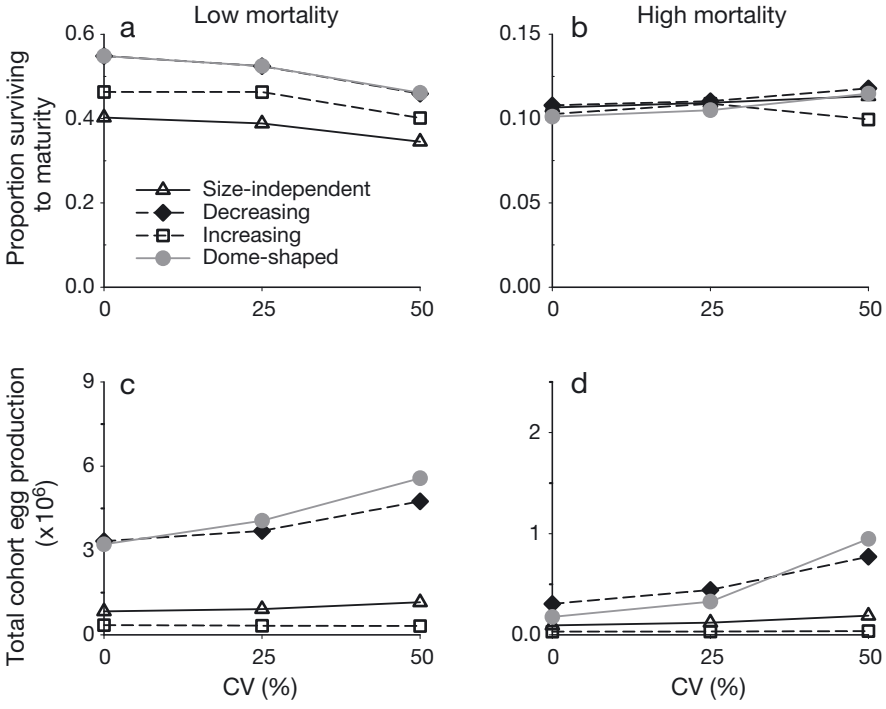

Fig. 3. Experiment 1: (a,b) mean proportion of individuals surviving to maturity, and (c,d) mean total cohort egg production for different degrees of variability among individuals (CV) under the low and high mortality rate versions of the 4 different types of mortality curves (see Fig. 1). All simulations were performed using the random genetic makeup, and under favorable environmental conditions (warm temperature of 24°C and high phytoplankton concentration of 1.0 mgC l^{-1})

CV had larger effects on total cohort egg production than on survival, and the magnitude of the effects on total cohort egg production depended on the type of mortality curve and the mortality rate (Fig. 3c,d). Total cohort egg production increased more with increasing CV for the decreasing and dome-shaped mortality curves than for the size-independent and increasing mortality curves, and the relative increase was greater under high mortality than under low mortality. For example, under the dome-shaped mortality curve, total cohort egg production from CV = 0 to 50% was about 5-fold higher under high mortality (1.8×10^5 under CV = 0 to 9.5×10^5 under CV = 50%), but only 1.75 times higher under low mortality (3.2×10^6 under CV = 0 to 5.6×10^6 under CV = 50%).

The effects of CV on total cohort egg production were due to the selection of traits of individuals that resulted in fast growth. Size-independent, decreasing, and dome-shaped mortality curves acted to select individuals with high ingestion rates (large I_{max} and large α) and low metabolic costs (small β_1), resulting in individuals that reached maturity at a larger body size and at a younger age. The degree of selection was stronger with increasing CV (Fig. 4). The selection was strongest for I_{max} and under the high mortality rates (Fig. 4b), but was also apparent for the other traits (Fig. 4). To illustrate, under the high mortality version of the dome-shaped mortality, the individuals that survived to maturity had averaged I_{max} values that were 42% higher under CV = 0 compared to CV = 50% (1.2 versus 1.7; Fig. 4b), averaged α values that were 9% higher (0.0068 versus 0.0074; Fig. 4d), and averaged β_1 values that were 10% lower (0.132 versus 0.119; Fig. 4f).

The selection for fast growers resulted in earlier maturation and higher individual egg production, which lead to higher total cohort egg production. For all combinations of mortality rate and the size-independent, decreasing, and dome-shaped mortality curves, individuals matured earlier and had higher peak daily cohort egg production under a CV = 50% versus a CV = 0 (Fig. 5a–f). For example, under the high mortality version of the dome-shaped curve, individuals initiated reproduction an average of 4 d earlier and peak egg production more than doubled (Fig. 5f); total cohort egg production increased from 1.8×10^5 to 9.5×10^5 eggs (Fig. 3d).

The effect of CV on trait selection and daily cohort egg production under the increasing mortality curve differed from the other mortality curves. Increasing mortality with size selected for individuals with higher metabolic costs (Fig. 4e,f), the opposite of the direction of selection for this trait under the other 3 mortality curves. Selection for ingestion rates was also weakest under increasing mortality than under the other mortality curves (Fig. 4a,b). These traits still resulted in earlier initial reproduction (Fig. 5g,h); however, the net effects of the traits did not cause higher peak values of daily cohort egg production (Fig. 5g,h), and total cohort egg production was similar for all values of CV (Fig. 3c,d).

λ was affected by both CV and mortality type (Fig. 6). Under low mortality rates (Fig. 6a), the spread of the lines (mortality type) was greater than the change in any given line (CV effect), while under high mortality rates (Fig. 6b), the increase in λ with CV under decreasing and dome-shaped mortality

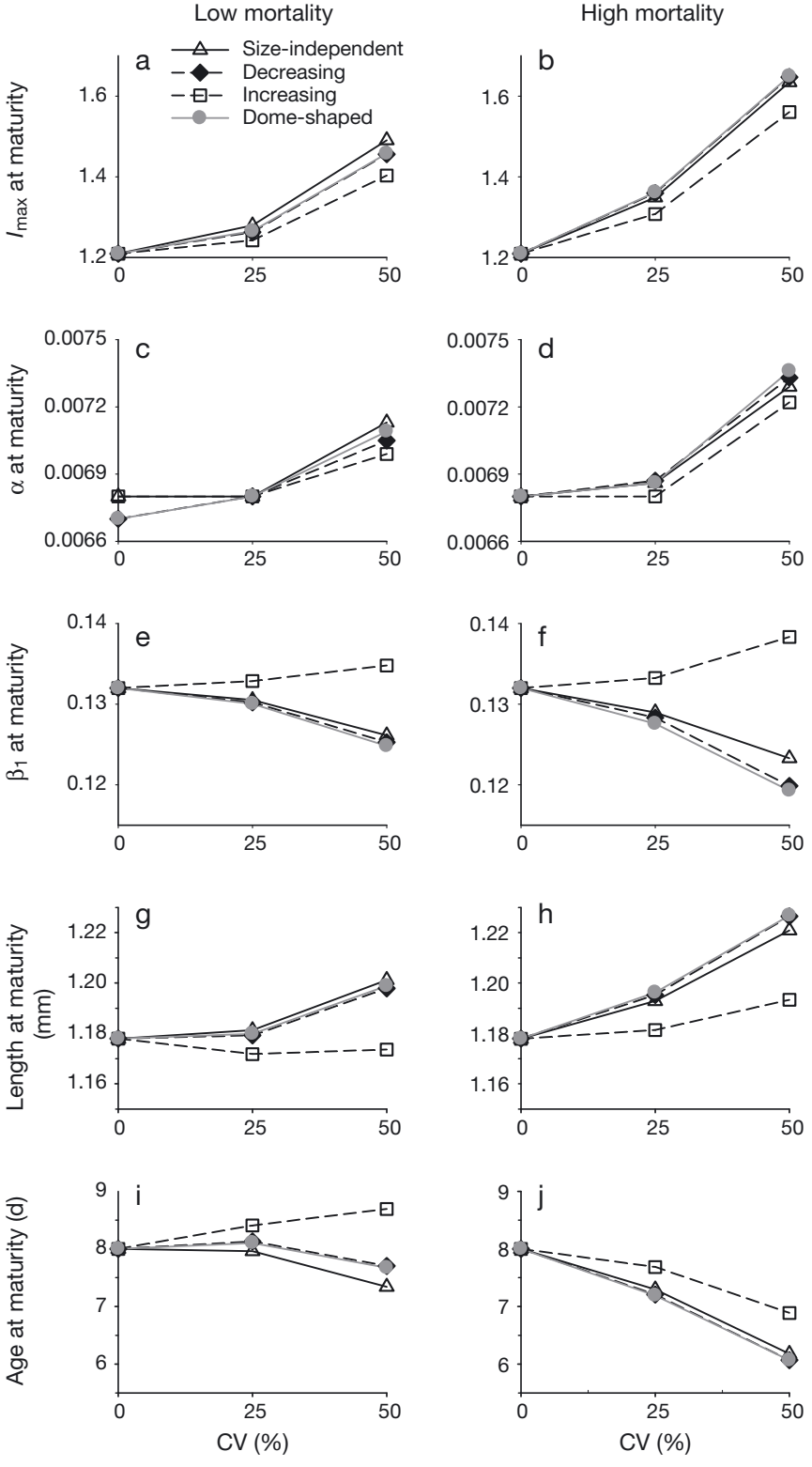

Fig. 4. Expt 1: model predictions of the mean traits of survivors to maturity for different degrees of variability (CV) among individuals under low and high mortality rates for 4 mortality curves (see Fig. 1). All simulations were performed using the random genetic makeup, under favorable environmental conditions. See Table 1 for definitions of I_{max}, α and β_1

was equal to or greater than the effect of mortality type. Under both low and high mortality, λ was highest for the decreasing and dome-shaped mortality curves and lowest with the increasing mortality curve. While there was essentially no effect of CV on λ under the low mortality rate, when the mortality rate was high, λ increased with CV by between 16% (increasing mortality curve) and 49% (dome-shaped mortality curve) from the CV = 0 to CV = 50% simulations.

Experiment 2: genetic makeup

Correlated genetic makeup increased the effects of CV relative to the effects predicted under the random genetic makeup in most simulations, particularly under high mortality rates (Fig. 7). Under low mortality, the correlated genetic makeup had a relatively small increasing effect on total cohort egg production (Fig. 7e,f) and λ (Fig. 7i,j) for the size-independent, decreasing, and dome-shaped mortality curves, with no effects predicted for the increasing mortality curve (blue lines). Under high mortality (Fig. 7), survival, total cohort egg production and λ increased with the correlated genetic makeup relative to the random genetic makeup with the decreasing, dome-shaped, and size-independent mortality types. For example, under high mortality and the decreasing mortality curve, λ increased from 1.63 at a CV = 0 to 2.67 at a CV = 50% under the correlated genetic makeup, which was a larger increase than the change from 1.63 to 2.21 predicted under the random genetic makeup. As under low mortality, genetic makeup had little effect on survival, total cohort egg production, and λ under high mortality with increasing mortality with size (Fig. 7c,g,k).

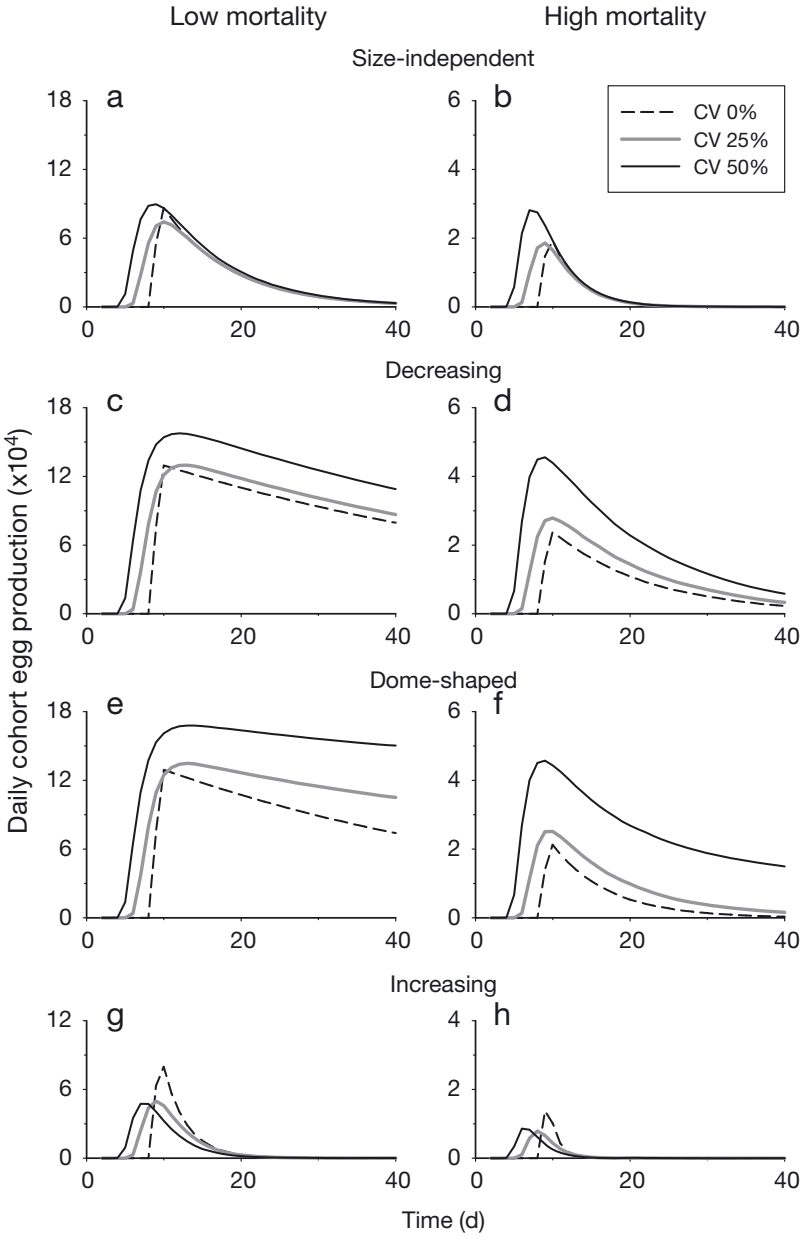

Fig. 5. Expt 1: daily cohort egg production over time for different degrees of variability among individuals (CV) for the 4 mortality curves (see Fig. 1) under low and high mortality rates. All simulations were performed using the random genetic makeup, and under favorable environmental conditions. We show data using lines instead of predicted points for clarity

Expt 3: unfavorable environmental conditions

The subtle but consistent effects of CV on cohort dynamics were robust to environmental conditions, as the same patterns predicted under the favorable environmental conditions (Expt 1) were also predicted under the poor environmental conditions (Fig. 8). The effects of CV on survival, total cohort egg production, and λ were stronger, however, under poor environmental conditions compared to under favorable environmental conditions within a given mortality rate and mortality type. We use the high mortality rate with the decreasing mortality curve as an example. When conditions were unfavorable, survival from CV = 0 to 50% increased 315% (0.28 to 1.13%), total cohort egg production increased from 0 eggs to 27 756 eggs, and λ increased by 84% (0.59 to 1.09). In comparison, under the same mortality conditions but with favorable environmental conditions, survival increased by 9% (10.8 to 11.8%), total cohort egg production increased 150% (306 572 to 771 479 eggs), and λ increased by 35% (1.63 to 2.20). While survival, total cohort egg production, and λ were higher under more favorable conditions, the gains in these parameters as CV increased was greater under unfavorable conditions.

DISCUSSION

Our model results demonstrate the potential for individual-level variability in bioenergetic traits to cause small, but potentially important effects on zooplankton cohort dynamics. Populations with little variability among individuals could therefore have a lower probability of persistence under unfavorable or stressful conditions, and the range of conditions under which a population can persist may be partially governed by the degree of variability among individuals. We also showed that the degree of variability among individuals can also have relatively large effects on λ under stressful or unfavorable conditions, which can affect the rate of recovery from perturbation.

Variability among individuals and cohort dynamics

Increasing individual-level variability resulted in selection for individuals with bioenergetic traits for fast growth. Faster-growing individuals reached maturation younger and at a greater body length and weight, which increased both daily and total cohort egg production, resulting in increased λ. This effect

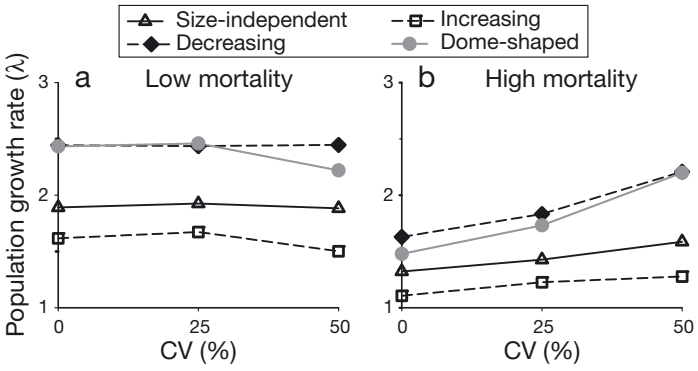

Fig. 6. Expt 1: model predictions of mean daily population growth rate (λ) for different degrees of variability among individuals (CV) under low and high mortality rates for 4 mortality curves (see Fig. 1). All simulations were performed using the random genetic makeup, under favorable environmental conditions

occurred under a wide range of simulated biotic and abiotic conditions.

In general, selection for high ingestion and low metabolic cost individuals was strongest under stressful conditions (poor environment and high mortality), and with size-dependent predation modeled with decreasing and dome-shaped mortality curves. Selection was apparent (albeit subtle) even under the simple conditions of size-independent mortality and favorable environmental conditions, as long as mortality rate was high. As expected, the correlated genetic make-up increased the effects of selection under many conditions. While some of the effects on λ were modest, small increases in values of daily λ can quickly (over days or weeks) translate into significant increases in population abundance. For example, λ increased from 1.63 under CV = 0 to 2.21 under

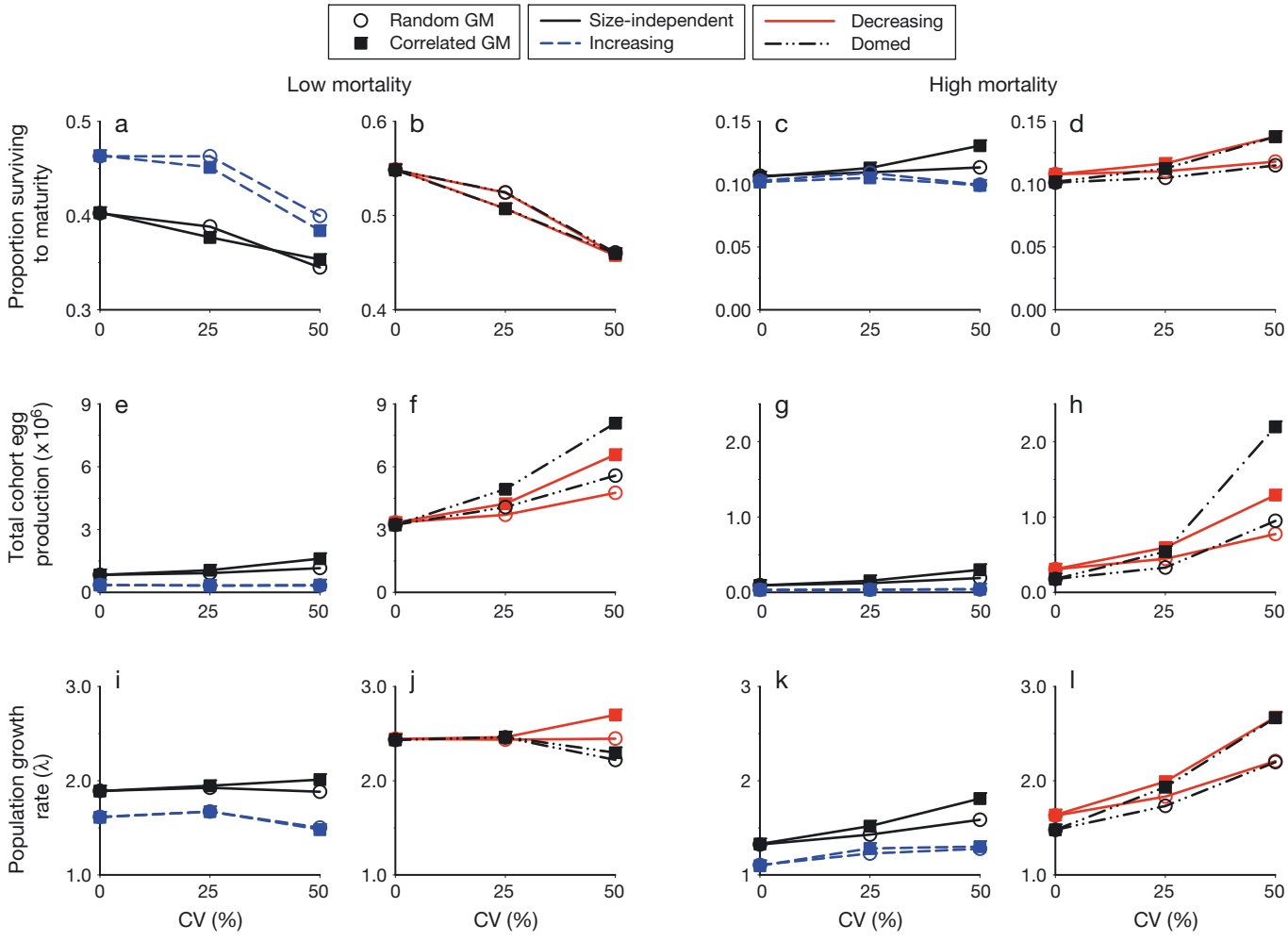

Fig. 7. Expt 2: model predictions of the mean proportion of individuals surviving to maturity, cumulative cohort egg production, and daily population growth rate (λ) for different degrees of variability among individuals (CV) for the 4 different types of mortality curves (see Fig. 1) for low and high mortality rates under random and correlated genetic makeups. All simulations were performed using favorable environmental conditions

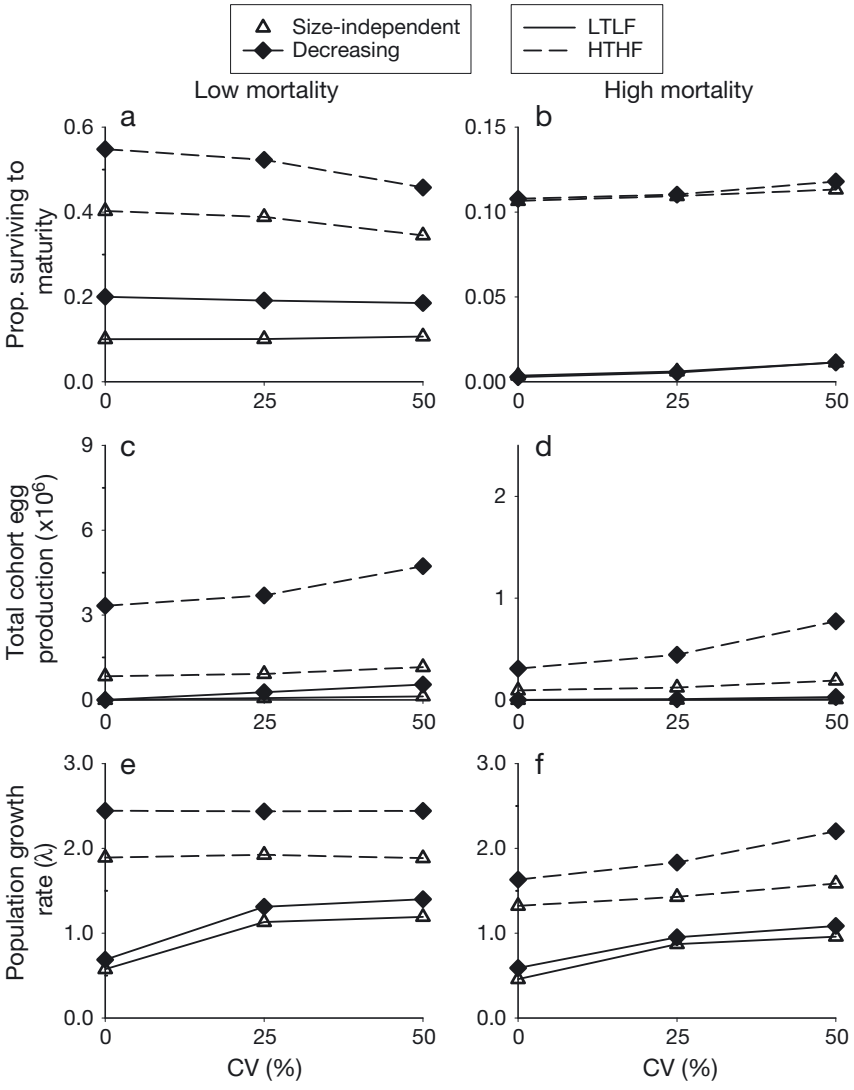

Fig. 8. Experiment 3: model predictions of (a,b) the mean proportion of individuals surviving to maturity, (c,d) cumulative cohort egg production, and (e,f) daily population growth rate (λ) for different degrees of variability among individuals (CV) for 4 different environmental conditions, low and high mortality rates, with size-independent and decreasing mortality curves. The 4 environmental conditions were all combinations of 2 temperatures (cold, 12°C and warm, 24°C) and 2 phytoplankton concentrations (low, 500 µgC l^{-1}; high, 1000 µgC l^{-1}); LT: low temperature; HT: high temperature; LF: low food concentration, HF: high food concentration. The combination of warm temperature and high phytoplankton concentration corresponds to the favorable conditions used in previous (Expts 1 and 2) simulations. Only LTLF and HTHF conditions are shown for simplicity. All simulations were performed using the random genetic makeup

CV = 50% in simulations with decreasing mortality with size, a high mortality rate and random genetic makeup (Fig. 5b). After 10 d, this would result in a cohort with 20 times the number of survivors. For example, a cohort started with 2 individuals would result in 5491 survivors after 10 d for CV = 50% versus 263 individuals for CV = 0. For a species with a short generation time, such as the copepod *Acartia tonsa*, the changes in λ simulated here could rapidly translate into meaningful differences in monthly and seasonal population abundances.

When environmental conditions were favorable and mortality rate was low, there was little or no gain in λ with increasing CV (Figs. 6a, 7i,j & 8e). Variability among individuals in terms of their traits, whether they be morphological, bioenergetic, or genetic, has been discussed as effective 'insurance' against stressful or changing environmental conditions (Kendall & Fox 2002, Hughes & Stachowicz 2004, Schindler et al. 2010). In contrast, populations experiencing optimal conditions may be successful without much variability among individuals, as long as the favorable conditions persist. Classic examples of this are amictic organisms such as rotifers or cladocerans, whose asexual reproduction produces clones of the parent under stable and favorable environmental conditions. These organisms then switch to sexual reproduction, and its accompanying genetic diversity, when conditions become unfavorable (King 1970, Serra & King 1999).

In our analysis, the type of size-dependent mortality had a large effect on survival, reproduction, and λ and on selection for fast growers. This finding suggests that temporal and spatial variability in abundant predators can have large effects on their prey populations based upon which prey individuals are selectively removed from the population by the predator. Climate change, fisheries exploitation, and nutrient enrichment are all expected to affect the relative abundances of various zooplanktivorous consumers (e.g. Purcell & Decker 2005, Hay 2006, Richardson et al. 2009). Our results suggest the combination of overall mortality rates and the size-selectivity of the predator field can have ecologically important effects on zooplankton population dynamics. Variability among individuals in the prey population may therefore be increasingly important as the predator field and resulting prey mortality rates change.

Interestingly, survival to maturity was unaffected by CV. We expected survival to be affected because we examined cohort dynamics under a variety of mortality curves and high and low mortality rates. These results suggest that individual-level variability should be examined for possible effects throughout the life cycle, and that the traits of the individuals that survive may have more important effects on population dynamics than the total number or proportion of individuals that survive. Because individuals that grew and reached maturity faster were the ones who survived in our model analysis, increasing CV manifested its greatest cohort effects on reproduction. In natural populations, these individuals that survive to mature and reproduce faster than others should have a disproportionate representation in future generations.

We examined whether the effects of CV described above were robust under 3 additional conditions: density-dependence, time-varying environmental conditions, and individual-level variability in κ. Density-dependent prey dynamics were simulated by representing phytoplankton (food) concentrations (x in Eq. 3) as logistic growth with zooplankton consumption as an additional mortality term; this resulted in a reduction in phytoplankton concentration during peak copepod cohort biomass. We used an r of 0.8 at 18°C and then adjusted this using a Q_{10} = 2.0 to our 12°C and 24°C, and used a carrying capacity in the logistic growth equation of 500 µg C l^{-1} under low food conditions and 1000 µg C l^{-1} under high food conditions.

Density-dependence prevented survival under favorable conditions due to high cohort predation pressure on the phytoplankton, and slower growth but reasonable survival under other conditions. When conditions were favorable (high temperature, high food, low mortality), and with decreasing or dome-shaped mortality, the cohort was able to graze the phytoplankton faster than they could grow, eventually driving phytoplankton concentrations to zero within the second week of the simulation. Some individuals reached maturity and reproduced for a week or more, but the cohorts were all decreasing ($\lambda < 1.0$) as a result of their overgrazing. Under all other conditions, however, zooplankton reduced the phytoplankton concentration a maximum of about 35% for 5 to 10 d (occurring between days 1 and 25, depending upon the simulation) before phytoplankton concentration began to increase again.

We repeated simulations from Expt 1, selecting simulations that showed larger effects of CV on λ, but now with density-dependence operating. The patterns in the results for the effects of CV = 0 versus CV = 50% on survival, cohort egg production, and λ were very similar to those obtained in Expt 1 under density-independent prey dynamics. For example, under density-independence and with the dome-shaped mortality curve (with random genetic makeup, high mortality, and high temperature and food levels), λ increased from 1.48 to 1.73 to 2.20 with increasing CV (0 to 25% to 50%) under density-independence (gray circles in Fig. 6b) and from 1.46 to 1.72 to 2.18 under density-dependence (results not shown).

We also tested the effect of adding time-varying environmental conditions on the predicted effects of CV on survival, total cohort egg production, and λ. In these simulations, we varied temperature on a daily basis, and food level on an hourly basis, with the assumption that zooplankton will encounter patchy conditions and more rapid changes in food levels than in temperature. We allowed each variable to vary each hour or day around its mean for the simulation. We simulated all combinations of low and high food levels, low and high temperatures, and with variability in food at CV of 10 or 25% and temperature as ±1° or ±2°C. These values were chosen to represent the hourly to daily variability in conditions a copepod could experience (e.g. Beaven 1960, Saiz & Tiselius 1993, Bochdansky & Bollens 2004). All simulations used random genetic makeup and the high dome-shaped mortality. Adding random variation to temperature and food level had relatively small effects on predicted values and did not change our conclusions about how CV affects survival, total cohort egg production, and λ. Our earlier results with fixed temperature and food had λ increasing from 1.47 to 1.74 to 2.19 with CV = 0, 25, and 50% (gray circles in Fig. 6b). With temperature and food both allowed to vary, λ values showed very similar increases with increasing CV of the bioenergetic traits (1.48 to 1.75 to 2.21 for the lower CV on temperature and food, and 1.50 to 1.76 to 2.22 for the higher CV on temperature and food). Additional simulations would be needed to evaluate how more complicated temporal patterns in temperatures and food could further affect model results, but our general conclusions would likely remain the same.

Finally, in order to further explore the importance of variability in individual traits, we varied an additional bioenergetics trait, κ, among individuals the same way we varied the other bioenergetics traits. We varied κ with CVs of 7.5 and 15% based upon reported estimates of the amount of carbon in crustaceans that is accumulated in the carapace com-

pared to the body (Hessen & Rukke 2000, Anderson et al. 2005). As with dynamic environmental conditions, we simulated all combinations of low and high food levels and temperature using random genetic make-up and the high version of dome-shaped mortality. When we added variability in κ, the general result was higher survival, higher total cohort egg production, and higher λ, but there were no major effects on how CV affected these variables. For example, variability in κ resulted in higher values of λ at all levels of CV, but without changing the pattern of λ increasing with CV. For example, when CV = 0 for κ, λ increased from 1.47 to 1.74 to 2.19 with increasing CV (0, 25%, and 50%) on the other bioenergetics traits (I_{max}, α, β_1 and β_2). Similarly, when CV = 15% for κ, λ increased from 2.49 to 2.71 as CV increased from 0 to 50% on the other bioenergetics traits. The remaining bioenergetics parameters were either implicitly varied as part of other traits that affect assimilation rate (γ has the same effect as I_{max}) or had very low reported variability (egg weight, see Kiørboe et al. 1985, Kleppel 1992).

We confirmed that our model-simulated values of ingestion and metabolism were consistent with available information by comparing predicted and reported growth efficiencies (Table 2). The published values for metabolic rates in *Acartia tonsa* to which we have compared our values are mostly at temperatures more favorable for this species (18 to 22°C); below these temperatures, our simulated metabolic rates are temperature-adjusted and reduced. We also compared model-generated and reported values of growth efficiency (K_1). Growth efficiency was computed in the model as the change in weight (μgC) divided by amount ingested (μgC) in a day for individuals of a range of sizes (nauplius, copepodite, and mature adult represented by individuals weighing 0.2, 3.0 and 6.0 μgC respectively), under all combinations of the simulated environmental conditions (low and high food, cold and warm temperature). For the range of temperatures we modeled (12 to 24°C), our simulated growth efficiency values ranged from 25 to 40%. Reported values from the literature for *A. tonsa* range from 10 to 55%, over a narrower range of temperatures (16 to 20°C) than we used. Growth efficiency is quite variable in this species and across studies, and our modeled values were within the range reported for *A. tonsa* (Table 2).

While the model formulation and parameter values we used are sufficient for our somewhat theoretical comparative analysis, further applications of this model, especially for site-specific or species-specific analyses, should include an evaluation of the model equations and evaluation of the parameter values. For example, in some applications, it may be important to include an ingestion or activity effect on metabolism (Kiørboe et al. 1985, Thor et al. 2002). Similarly, the specific parameter values we used via our calibration may need to be made site-specific to accommodate local effects and environmental conditions other than those we examined.

Our modeling approach, consisting of seeding a cohort with individuals differing in a variety of traits and allowing the environmental conditions to drive the final makeup of the cohort, is similar to methods used successfully to model plankton community structure (e.g. Follows et al. 2007, Gentleman et al. 2008, Neuheimer et al. 2010). Model predictions based upon populations incorporating variation in traits or genetic diversity within populations, or species diversity within communities, have been shown to generate realistic behavior that corresponds well to field observations of spatial and temporal abundance patterns (e.g. Clark 2003, Scharf et al. 2006, Kramer-Schadt et al. 2009). As our knowledge of the effects of trait variation and genetic diversity on community and ecosystem function in field populations increases (e.g. Hanski & Saccheri 2006, Hughes et al. 2008, Messier et al. 2010), models incorporating variability into populations and communities, and allowing emergent properties to form from model simulations, should bring even more insight into the links between ecological- and evolutionary-scale processes.

Implications for populations under stress

Under unfavorable abiotic and biotic conditions, increases in λ with variability among individuals as seen in these simulations can be important to population dynamics, and may buffer their responses to stressful conditions. This may be because, at least in the short term, variability among individuals in ecologically relevant traits can effectively achieve the same results as might be found in a cohort where individuals each have broad physiological tolerances (longer term consequences are discussed below). Buffering of the response to stressful or variable conditions need not arise through a single individual tolerating many conditions, but can arise because of a higher likelihood that at least some individuals in the population will do well under the range of environmental conditions experienced (Hanski 1996, Bown et al. 2007, Reed et al. 2007). Greater variability among individuals has been shown to increase model

population persistence when compared to populations of individuals with identical values of traits. With variability among individuals, a subset of individuals were able to survive and reproduce, enabling even populations reduced to small numbers to rebound in some cases, whereas populations with no variability among individuals experienced rapid extinction once conditions become unfavorable for reproduction (Uchmanski 1999). An analogous situation of individual variability buffering population responses can be found with community stability being increased through complementary responses by different species (Doak et al. 1998, Naeem 1998, Schindler et al. 2010). While we have modeled the effects of variability among individuals on cohort dynamics under a range of environmental conditions, it would be interesting to explore these effects at the population and community levels.

The simulations presented here represent constant selective pressures acting upon a cohort, resulting in a cohort with reduced variability among the individuals that survive to maturity. The time scale involved in many of our response variables is on the order of days to weeks. We expect that *Acartia tonsa* individuals experience fluctuations in some field conditions (e.g. phytoplankton concentrations) at similar time scales, while other conditions (e.g. water temperature) would be relatively constant on the ecological time scale of a cohort but will vary among generations. As one example of variable field conditions, the dominant predators of *A. tonsa* change throughout the season when the copepod is most abundant. In the Chesapeake Bay, the relative abundances of ctenophores, scyphomedusae, and zooplanktivorous fishes vary during the late spring through early autumn period in which *A. tonsa* is the dominant copepod (Olson 1987, Baird & Ulanowicz 1989, Cowan & Houde 1993). In Narragansett Bay, Rhode Island, USA, the ctenophore *Mnemiopsis leidyi* is present in variable numbers from late spring or early summer through early fall, and fish predators such as the Atlantic menhaden *Brevoortia tyrannus* are common between May and November (Kremer 1979, Deason 1982, Sullivan et al. 2001). These predators each feed most heavily upon different size classes of *A. tonsa*, such that the magnitude and size-selectivity of predation varies among cohorts within the year. If cohorts with a high degree of variability among individuals are more likely to persist under the range of environmental conditions experienced by multiple generations, then variability among individuals in a dynamic environment may be even more important than implied by our constant-environment simulations.

The maintenance of variability among individuals in populations

Conflicting forces can act on the maintenance of variability among individuals in a population. Variability can be decreased by selective forces, and our simulations demonstrated how individual traits can be selected for on the ecological time scale of a cohort, leaving a cohort with lower genetic variability in heritable traits to pass on to offspring. Over multiple generations, however, variability among individuals can be increased or maintained by temporally or spatially varying selective pressures. The possession of a 'seed bank' can also serve to maintain genetic diversity in a population over long periods of time (MacDonald & Watkinson 1981, Levin 1990, Koch et al. 2003). The equivalent of seed banks are common in many freshwater and marine planktonic copepods; *Acartia tonsa* itself produces resting (diapause) eggs that accumulate in the sediments and can remain viable through seasonally inhospitable conditions (Marcus 1991, Marcus et al. 1994). This can bring about the preservation of genetic variation in populations because genotypes that are disadvantageous under one set of environmental conditions may be able to repopulate under more favorable conditions (Hairston & DeStasio 1988, Marcus 1991, Hairston & Fox 2009). Short-term reduction in variability among individuals resulting from directional selection pressures as simulated in this paper could, therefore, be offset over longer time scales by the reintroduction of genotypes and the restoration of variability from seed banks, egg banks, or resting eggs (Hairston & DeStasio 1988, DeStasio 1989, Hairston & Kearns 2002). Migration can accomplish a similar reintroduction of variability in an environment with spatial variation in selective pressures. Isolated or fragmented habitats without significant immigration may, therefore, be at greater risk of retaining reduced genetic variability. This issue is of increasing concern today, when unexploited natural habitats are reduced in size and often separated from each other by distances that inhibit the natural flux of immigration and emigration.

CONCLUSIONS

Variability in traits among individuals is often not explicitly considered in analyses of zooplankton cohort and population dynamics. Our model results demonstrated how small changes in the bioenergetic traits of individuals in a cohort, leading to small

changes in the life history traits of surviving individuals, can have ecologically meaningful effects on cohort reproductive output and λ. The bioenergetic traits we varied among individuals are typically treated as the same fixed values for all individuals of the same size or age (van den Bosch & Gabriel 1994, Gentleman 2002, Gentleman et al. 2008). Our results were robust under a range of environmental conditions (and density-dependence), and illustrated the influence of individual variability on cohort dynamics across a wide range of abiotic and biotic conditions. The degree of variability in traits among individuals may be particularly important in populations experiencing unfavorable or stressful conditions, as these are conditions when λ is low and selection pressure is strongest. A high degree of variability in traits among individuals may provide buffering under new or dynamic environmental conditions, due to the increased possibility that the population includes at least some individuals capable of performing well as conditions change. Variability among individuals may, therefore, serve as a useful metric in assessing the health of local populations.

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Appendix 1.

Table A1. *Acartia tonsa* threshold molt carbon (S_T) required for molting, by stage. N = naupliar, C = copepodite

Stage	Threshold carbon (S_T) (µgC ind.$^{-1}$)
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

Table A2. Example of stage-based model for a simulation with CV = 25%, random genetic makeup, size-independent mortality, low mortality rate, and favorable environmental conditions (high food, high temperature). D_i = average molt duration (days); σ = daily survival rate; γ = proportion of daily survivors that molt; P_i = probability of remaining in a stage; G_i = probability of molting to the next stage; F_i = number of female eggs produced per female per day

Stage (*i*)	D_i	σ_i	γ_i	P_i	G_i	F_i
N1	0.466	0.996	0.087	0.909	0.087	0.000
N2	0.491	0.994	0.082	0.913	0.082	0.000
N3	0.529	0.995	0.077	0.919	0.076	0.000
N4	0.563	0.995	0.072	0.924	0.071	0.000
N5	0.602	0.995	0.067	0.928	0.066	0.000
N6	0.639	0.995	0.063	0.932	0.063	0.000
C1	0.679	0.995	0.059	0.936	0.059	0.000
C2	0.729	0.995	0.055	0.940	0.055	0.000
C3	0.755	0.995	0.053	0.942	0.053	0.000
C4	0.811	0.995	0.049	0.946	0.049	0.000
C5	0.834	0.995	0.047	0.947	0.047	0.000
C6 (adult)	21.030	0.917	0.000	0.917	0.000	11.810

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