The effects of climate change on density-dependent population dynamics of aquatic invertebrates

Edmund M. Hart and Nicholas J. Gotelli

E. M. H (.1@ m.) N. J. G , D. B , . m , B , 05404, A.

Global climate change has the potential to alter aquatic communities through changes in evapotranspiration and increased variability in precipitation. We used aquatic mesocosms to test the impacts of variable precipitation on population dynamics of common mosquito (Culicidae) and midge (Chironomidae) larvae that inhabit vernal pools. In a mixed deciduous forest in northern Vermont, USA, we orthogonally crossed seven levels of mean water level (increased rainfall) with seven levels of water level coe cient of variation (more variable rainfall) to simulate a broad array of climate change scenarios in 49 experimental mesocosms.

e average abundance of Culicidae was highest at low water levels, whereas the average abundance of Chironomidae was highest at higher water levels and low variability in water level. Treatments and environmental and spatial covariates collectively explained 49% of the variance in mean abundance. For both taxa, we fit hierarchical Bayesian models to each 16-week time series to estimate the parameters in a Gompertz logistic equation of population growth with density dependence. We found that Culicidae population growth rate increased with decreasing water levels and that 87% of the variance in Chironomidae density dependence could be explained by treatment. Collectively, these results suggest that climate change can alter abundances aquatic invertebrate taxa but not necessarily through the same mechanism on all populations. In the case of Culicidae the abundance is a ected by changes in growth rate, and in Chironomidae by changes in the strength of density dependence.

Over the past decade, ecologists have used field and laboratory experiments to document population and community responses to global climate change, including responses to elevated CO_2 (Ainsworth and Long 2005), increased temperature (Visser and Holleman 2001), and increased variability in precipitation (Suttle et al. 2007). Some correlative studies have also examined the relationship between climate and population dynamics (Mysterud et al. 2001, Halkka et al. 2006, Turner et al. 2006, Tavecchia et al. 2007, Lima et al. 2008, Ogutu et al. 2008) by testing for relationships between time series of abundance and environmental covariates (Ives 1995, Ådahl et al. 2006). Experimental studies of the e ects of climate change may provide stronger evidence and more powerful results for forecasting (Krebs and Berteaux 2006), but they are still uncommon (Richmond et al. 2007). Using a manipulative field experiment, we asked how climate change impactson the mean and variance of water level a ect the population dynamics of aquatic invertebrates in aquatic mesocosms.

Studies on population dynamics and climate change usually rely on either long data sets that span contemporary climate change (Adler and HilleRisLambers 2008, van de Pol et al 2010) or time series data that span natural climatic fluctuation such as the North Atlantic Oscillation (NAO) (Sæther et al 2000, Coulson et al 2001). ese

studies construct models that examine how population size and density dependence track changes in the mean value of a variable such as NAO index (Sæther et al 2000), temperature or precipitation (Adler and HilleRisLambers 2008). While the mean values of precipitation and temperatures are increasing due to climate change, the variance around those means is also expected to increase (Hayhoe et al 2008). It is equally important therefore that we understand how both the mean and variance of a variable a ect population dynamics (Benedetti-Cecchi 2003). To that end van de Pol et al (2010) used a long term data set for oyster catchers to construct demographic that included both mean temperature and temperature variability. ey found that temperature mean was more important than variability for population persistence, but variability in temperature was important for juvenile survivorship. e results we present here complement work such as this by testing the importance the mean and variance in climate variables with a manipulative field experiment. We created forty-nine artificial vernal pond mesocosms in northern Vermont, and fully crossed seven levels of mean water level with seven levels of the coe cient of variation (CV) in water depth to mimic climate change scenarios in vernal ponds due to altered precipitation. en using non-destructive in-situ sampling and we monitored populations of larval Culicidae

and Chironomidae over the course of a single field season. With this data we constructed population dynamic models for each taxa and examined how model parameters varied with changes the mean and variance of water level..

We predicted that both taxa would have increased population size and decreased density dependence in deeper and less variable mesocosms. Deeper water levels should increase resources, habitat volume and thereby reducing density dependent mortality, whereas a higher CV generates more variable environments which tends to increase extinction rates and population variability (Boyce et al 2006, van de Pol et al 2010), especially in response to changes in rainfall (Drake 2005).

Methods

Study system

Regional climate change models predict a warming of 2° to 3.5°C by 2100 under low emissions scenarios, and an even larger increase under high emission scenarios (Frumho et al. 2006). Climate change scenarios for the northeast USA also predict an increased water budget in the winter/spring and increased deficit in the summer/fall (Moore et al. 1997). Precipitation events are likely to become more variable, with longer periods of drought followed by more intense deluges (Sun et al. 2007, Kendon et al. 2008). Vernal ponds are fishless habitats that fill in the spring (vernal) or fall (autumnal) and hold water for at least four months (Zedler 2003) and represent ideal systems to study the effects of climate change. Climate change will alter these systems through increased evapotranspiration and more variable precipitation. Increased winter precipitation will increase initial pond volume, and more variable spring summer rainfall combined with greater evapotranspiration will increase the variability through the season of pond water level.

Our mesocosms supported a variety of invertebrate taxa that are found in natural vernal pools. Non-destructive insitu field sampling of tubs did not allow us to consistently distinguish individuals to genus and species, so we restricted our analyses to the family level. e insect fami-

mesocosms had a relatively small area, but did have realistic depth ranges. Mesocosms were laid out in April 2007 in an octagonal array, with each tub approximately 1.5 m from its nearest neighbor. Plastic fencing was installed around the entire array to prevent dogs and other large vertebrates from disturbing the mesocosms. In contrast to many classic cattle-tank experiments (Wilbur 1987), our mesocosms were left open for the duration of the experiment to allow for external colonization. Each of the 49 unique treatments was assigned randomly to one of the replicates. We seeded each mesocosm with approximately 300 ml of water from a well-mixed plankton tow and 4 l of an innoculum of detritus and insects from a nearby vernal pond. We filled each mesocosm with leaf litter from the surrounding forest to achieve a detrital depth of 1–2 cm. All mesocosms were then filled to their initial depth with filtered water from a nearby spring-fed well. We measured water levels weekly, and adjusted them according to their prescribed treatment by either adding well water, or drawing water levels down with a 1136 lph battery-powered pump. e pump hose was covered by two layers of 1 mm mesh to prevent macro-invertebrate capture. At each census, we also measured pH, dissolved oxygen (DO), water temperature, air temperature and turbidity. We sampled each mesocosm by sweeping a 7.6 × 10 cm net (3 mm mesh) once through the water column, and once through the benthic material. To avoid destructive sampling, all animals were transferred to a sorting tray in the field, counted, identified to the family level, and immediately returned to their mesocosm. We sampled invertebrates, measured abiotic variables, and then adjusted water levels weekly from 5 April – 28 August 2007, yielding 16 consecutive observations for each container.

Statistical analysis

We encountered some zeroes in our weekly counts so we first added 1 to every number and then log transformed them to normalize our data (McArdle et al. 1990) in all our analyses. Average abundances were calculated by taking the mean of transformed abundances, e ectively the geometric mean.

A erage pop la ion si e
With each mesocosm representing a single observation (n = 49), we next fit a multiple regression model with main e ects for mean water level (MWL) and CV (WLCV) and their interaction:

$$y_i = \beta_0 + \beta_1 \times MWL + \beta_2 \times WLCV + \beta_3 \times MWL \times WLCV + \epsilon_i$$

For each taxon, we calculated the R^2 of the fitted model and the statistical significance of the regression coe cients.

Effec s of en ironmen al co aria es on a erage ab ndance
In order to take both unknown spatial e ects and environmental covariates into account, we used backwards stepwise regression to select the best model out of all our measured covariates. e values for covariates represent the average of

sixteen measurements taken from each tub at the time we sampled invertebrates. e full general model was:

$$y_i = \beta_0 + \beta_1 \times MWL + \beta_2 \times WLCV + \beta_3 \times MWL \times WLCV + \beta_4 \times D.O. + \beta_5 \times pH + \beta_6 \times Air\ temp + \beta_7 \times Water\ temp$$

where MWL is mean water level, WLCV is water level CV, y

density dependent term $_{jk}$ on the log of the population size plus one at the previous time step $X_{[t-1]jk}$ is the logarithm of population size. We modeled the parameters   and   as multivariate normal variables. We modeled the effects of water level and CV as rescaled normal variables with a mean of 0.

$$
\begin{vmatrix} _{jk} \\ _{jk} \end{vmatrix} = \begin{vmatrix} \\ \end{vmatrix} + \begin{vmatrix} \\ \end{vmatrix} + \begin{vmatrix} \\ - \end{vmatrix} + \begin{vmatrix} \\ \end{vmatrix} \times \begin{vmatrix} - \\ - \end{vmatrix} \tag{5}
$$

Each term in Eq. 5 except for   was modeled as:

$$
B_j \quad MVN(U, \ _B) \tag{6}
$$

where $U = (0,0)$, and $_B$ is the variance-covariance matrix for the different effect sizes.   is formulation allowed us to measure the covariance between slopes and intercepts in the GL model.

We fit the models using Markov-chain Monte Carlo algorithms written in R 2.10 (R Core Development Team 2010) using Gibbs samplers. We ran three chains with random starting points and 10 000 iterations each with non-informative priors. Convergence was assessed by plotting MCMC output and checking for autcorrelation and poor sample mixing, as well as using Gelman and Rubin's convergence statistic (Gelman and Rubin 1992) in the R package coda (Plummer et al. 2006). Individual estimates of slope and intercept parameters were then tested against treatment in a two-factor response surface multiple regression.

Results

Average abundance

Abundance of each taxon, averaged across the entire time-series, was significantly affected by water-level treatments. For Culicidae, average abundance decreased with increasing water level ($_1 = -0.04$, $p = 0.008$) but was not significantly affected by water level CV ($_2 = -1.02$, $p = 0.21$; Fig. 1).   e model explained 27% of the total variation in average Culicidae abundance. For Chironomidae, average abundance was not affected by mean water level ($_1 = 0.006$, $p = 0.58$) but was affected by the CV of water level ($_2 = -2.26$, $p = 0.0005$). However, the interaction between mean water level and CV was significant ($_3 = 0.097$, $p = 0.006$) and abundance was unusually low when both mean water level and CV were low (Fig. 1).

e model explained 49% of the total variance in average Chironomidae abundance.

Effects of environmental covariates on average abundance

ere was a moderate degree of intercorrelation between abundances and measured environmental covariates (Table 1).

e model selection procedure identified the best model for Culicidae as:

$$
Culicidae_i = 10.2 - 0.02
$$

with an R^2 of 0.49. For Chironomidae the model selected was:

$$
Chironomidae_i = 1.5 + 0.00 \times MWL - 0.2 \times WLCV \\ + 0.1 \times MWL \times WLCV
$$

alsowith an R^2 of 0.49. Although each model was different, the two experimental treatment effects were always present in the final model. Culicidae responded to both treatments and a suite of environmental covariates as well as spatial location. Chironomidae, on the other hand, responded only to the treatments but not to any of the covariates.

Population dynamics and density dependence

Culicidae population growth rate   varied negatively with mean water level ($p = 0.0004$) with an R^2 of 0.43, and the density dependent term   varied negatively with both mean water level ($p = 0.006$) and CV ($p = 0.04$) with an R^2 of 0.18 (Fig. 2). Population growth rate   for Chironomidae did not vary consistently with treatment ($p = 0.07$ for mean water level and $p = 0.02$ for CV, $R^2 = 0.13$) (Fig. 2). However,

Table 1. Pearson correlation coeffecients between Culicidae and Chrionomidae abundance and environmental covariates and spatial coordinates of each mesocosm. Population averages represent the mean log abundance of all 16 time points for each mesocosm. Averages for other physical variables represent the mean over all sampling dates. Spatial coordinates represent the tubs position in a simple Cartesian grid-space. Significant Pearson product moment correlations (p < 0.05) are bold and italicized.

	Culicidae	Chironomidae	pH	Air temp	Water temp	DO	x-coord
Culicidae	–	–	–	–	–	–	–
Chironomidae	–0.21	–	–	–	–	–	–
pH	–0.24	0.05	–	–	–	–	–
Air temp	–0.06	–0.18	*0.32*	–	–	–	–
Watertemp	0.01	–0.25	0.24	*0.79*	–	–	–
DO	*0.37*	*0.39*	–0.10	*0.43*	*0.43*	–	–
x-coord	*0.32*	0.32	0.03	–0.27	–0.15	*0.32*	–
y-coord	–0.03	0.14	*0.44*	*0.86*	*0.73*	*0.46*	0.09

the density dependent term   for Chironomideae responded strongly to treatment ($R^2 = 0.87$). Density dependence was strongest at low water levels and high CV (p = 0.00001 for mean water level and p = 0.00001 for CV) (Fig. 2).

Discussion

Both mean abundance (Fig. 1) and population model parameters (Fig. 2) in Culicidae and Chironomidae had di er-ent responses to the same treatment combinations. Culicidae had high abundance at low mean water levels (Fig. 1), whereas Chironomidae supported our initial hypothesis and had high abundance at high water levels with low CV (Fig. 1).

Time-series trajectories of population change in individual treatments provide insight into how population growth a ects abundance (Fig. 3).Culicidae populations in di erent treatments showed similar population trajectories but with di erent growth rates ( ), which resulted in high abundance in low mean water level tubs (Fig. 3). In contrast, Chirono-midae abundance changed because of changes in the strength of density dependence ( ), with almost very weak density dependence in high mean water level and low CV treatments (dashed line Fig. 3).

   ese changes in population dynamic parameters that di er by taxa most likely reflect their di erent life histo-ries. We believe that the higher growth rate at lower water levels in Culicidae is caused by female oviposition choice

Figure 2. Estimates of the Gompertz logistic (GL) parameters for each treatment combination. Culicidae is in the left column with growth

because oviposition represents an increase in 'births' of the larval population (which itself does not reproduce in a mesocosm). Female oviposition choice in Culicidae is sensitive to the presence of predators (Kiflawi et al. 2003, Blaustein et al. 2004), conspecifics (Edgerly et al. 1998), and habitat nutrient quality (Reiskind and Wilson 2004, Mokany and Mokany 2006). Because predator density did not vary among our treatments, nutrient concentration and conspecific abundance probably increased oviposition rates in low water tubs. e lower mean water means increased nutrient concentrations because the detritus type and amount was held constant. Once those treatments developed an initial population, females may have been attracted to mesocosms with high densities of conspecific larva as an indicator of future larval success (Edgerly et al. 1998). Culicidae abundance also varied with spatial position, temperature and dissolved O_2 concentration in mesocosms, which may reflect direct and indirect e ects of our treatments on larval abundance and female oviposition choices.

cosm)w

water level (Fig. 2d). In contrast to the results for Culicidae, none of the measured covariates a ected Chironomidae abundance. Instead, the abundance levels were driven only by the two experimental treatments, suggesting that, that post-colonization processes related directly to water level and variability were most important for Chironomidae.

Four caveats apply to our experimental study. First, the sampling regime and population growth equations we used do not allow us to infer the precise mechanisms of density-dependence, because we cannot distinguish between e ects of migration from those of birth and death. Second, our mesocosms excluded amphibians and their larval stages, which act as important predators in many aquatic ecosystems (Wilbur 1987, Morin et al. 1988, Wilbur and Fauth 1990). We are currently running long-term experiments with larger experimental ponds that allow for amphibian migration. Finally, as in previous studies that used in situ sampling of invertebrates in the field (Gunnarson 1983, Caley 1995), it was necessary to lump species and genera into insect families. ere are many examples of species-level di erences among Culicidae (Spencer et al. 2002, Blaustein et al. 2004, Ellis 2008, Juliano 2009), so that density-dependence might be masked by pooling data at the family level. However it is di cult to see how pooling could

cause spurious patterns of density-dependence that systematically map onto different hydroperiod regimes (Fig. 2).

The fact that there were similar responses of the two families in different locations in the parameter space (Fig. 2, 4) also suggests that analyses are valid at the family level.

Finally we used a response surface design without replication. We had to choose between covering a larger parameter space or more replicates (Cottingham et al. 2005). We decided to cover a large parameter space because that would allow for the most robust inferences about future climates. One potential problem is that priority effects could result in alternative stable states (Chase 2003). However the patterns of abundance and population parameters measured across the treatment space suggest that the signal of hydroperiod is stronger than the noise from stochastically assembled communities (Chase 2010), although stochastic community formation cannot completely disregarded.

Our results support other correlative studies that suggest climate change, specifically changes in precipitation, can alter population dynamics (Coulson et al. 2001, Ogutu et al. 2008). We predict that with climate-induced decreases in mean water level and increases in variability, Culicidae will have increased population growth, and Chironimidae will show stronger density-dependence (Fig. 2), which could potentially increase the regional population size of Culicidae. Our results provide insights into the kind of population dynamics (Fig. 2), abundance patterns (Fig. 1) that can be expected with different climate change scenarios scenarios.

References

Ådahl, E. et al. 2006. From climate change to population change: the need to consider annual life cycles. – Global Change Biol. 12: 1627–1633.

Adler, P. B. and HilleRisLambers, J. 2008. The influence of climate and species composition on the population dynamics of ten prairie. – Ecology 89: 3049–3060.

Ainsworth, E. and Long, S. 2005. What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. – New Phytol. 165: 351–371.

Armitage, P. D. et al. 1994. Chironomidae: the biology and ecology of non-biting midges. – Springer.

Benedetti-Cecchi, L. 2003. The importance of the variance around the mean effect size of ecological processes. – Ecology 84: 2335–2346.

Berryman, A. A. 1999. Principles of population dynamics and their application. – Garland Science.

Blaustein, L. et al. 2004. Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. – Oecologia 138: 300–305.

Boyce, M. S. et al. 2006. Demography in an increasingly variable world. – Trends Ecol. Evol. 21: 141–148.

Burnham, D. and Sorensen, E. 2003. Vermont Wetlands Bioassessment Program: an evaluation of the cemical, physical and biological characteristics of seasonal pools and Northern White Cedar Swamps. – Vermont Dept of Environmental Conservation and Vermont Dept of Fish and Wildlife, Nongame and Natural Heritage Program, Waterbury, VT.

Caley, M. J. 1995. Community dynamics of tropical reef fishes: local patterns between latitudes. – Mar. Ecol. Prog. Ser. 129: 7–18.

Chase, J. M. 2003. Experimental evidence for alternative stable equilibria in a benthic pond food web. – Ecol. Lett. 6: 733–741.

Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. – Science 328: 1388–1391.

Colburn, E. 2004. Vernal pools: natural history and conservation. – McDonald and Woodward Publishing Company.

Cottingham, K. L. et al. 2005. Knowing when to draw the line: designing more informative ecological experiments. – Front. Ecol. Environ. 3: 145–152.

Coulson, T. et al. 2001. Age, sex, density, winter weather and population crashes in Soay sheep. – Science 292: 1528–1531.

Dennis, B. and Taper, M. L. 1994. Density-dependence in time-series observations of natural populations: estimation and testing. – Ecol. Monogr. 64: 205–224.

Drake, J. M. 2005. Population effects of increased climate variation. – Proc. R. Soc. B 272: 1823–1827.

Edgerly, J. S. et al. 1998. A seasonal shift in egg-laying behaviour in response to cues of future competition in a treehole mosquito. – J. Anim. Ecol. 67: 805–818.

Ellis, A. M. 2008. Incorporating density dependence into the oviposition preference – offspring performance hypothesis. – J. Anim. Ecol. 77: 247–256.

Frumhoff, P. et al. 2006. Climate change in the US Northeast. – Union of Concerned Scientists.

Gelman, A. and Rubin, D. B. 1992. Inference from iterative simulation using multiple sequences. – Stat. Sci. 7: 457–472.

Graham, A. 2008. Mosquitoes of Vermont. – Vermont Agency of Agric., Div. of Agric. Manage. and Environ. Stewardship, Montepelier, Vermont, USA.

Gunnarsson, B. 1983. Winter mortality of spruce living spiders: effect of spider interactions and bird predation. – Oikos 40: 226–233.

Halkka, A. et al. 2006. Lagged effects of North Atlantic Oscillation on spittlebug *P.....m.* (Homoptera) abundance and survival. – Global Change Biol. 12: 2250–2262.

Hayhoe, K. et al. 2008. Regional climate change projections for the northeast USA. – Mitigation Adaptation Strategies Global Change 13: 425–436.

Hooper, H. L. et al. 2003. The influence of larval density, food availability and habitat longevity on the life history and population growth rate of the midge *C.....m.......* – Oikos 102: 515–524.

Husak, G. J. et al. 2007. Use of the gamma distribution to represent monthly rainfall in Africa for drought monitoring applications. – Int. J. Climatol. 27: 935–944.

Inouye, B. D. 2001. Response surface experimental designs for investigating interspecific competition. – Ecology 82: 2696–2706.

Ives, A. R. 1995. Predicting the response of populations to environmental change. – Ecology 76: 926–941.

Ives, A. R. et al. 2003. Estimating community stability and ecological interactions from time-series data. – Ecol. Monogr. 73: 301–330.

Juliano, S. A. 2009. Species interactions among larval mosquitoes: context dependence across habitat gradients. – Annu. Rev. Entomol. 54: 37–56.

Kendon, E. J. et al. 2008. Robustness of future changes in local precipitation extremes. – J. Climate 21: 4280–4297.

Kiflawi, M. et al. 2003. Oviposition habitat selection by the mosquito *C.............* in response to risk of predation

and conspecific larval density. – Ecol. Entomol. 28: 168–173.

Krebs, C. J. and Berteaux, D. 2006. Problems and pitfalls in relating climate variability to population dynamics. – Climate Res. 32: 143–149.

Lima, M. et al. 2008. Chihuahuan Desert kangaroo rats: nonlinear e ects of population dynamics, competition and rainfall. – Ecology 89: 2594–2603.

McArdle, B. H. et al. 1990. Variation in the size of animal populations – patterns, problems and artifacts. – J. Anim. Ecol. 59: 439–454.

McCoy, M. W. and Bolker, B. M. 2008. Trait-mediated interactions: influence of prey size, density and experience. – J. Anim. Ecol. 77: 478–486.

Mokany, A. and Mokany, K. 2006. E ects of habitat permanence cues on larval abundance of two mosquito species. – Hydrobiologia 563: 269–276.

Moore, M. V. et al. 1997. Potential e ects of climate change on freshwater ecosystems of the New England/Mid-Atlantic Region. – Hydrol. Processes 11: 925–947.

Morin, P. J. et al. 1988. Competition between aquatic insects and vertebrates – interaction strength and higher-order interactions. – Ecology 69: 1401–1409.

Mysterud, A. et al. 2001. Nonlinear e ects of large-scale climatic variability on wild and domestic herbivores. – Nature 410: 1096–1099.

Ogutu, J. O. et al. 2008. Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. – J. Anim. Ecol. 77: 814–829.

Plummer, M. et al. 2006. CODA: convergence diagnosis and output analysis for MCMC. – R News 6: 7–11.

Reiskind, M. H. and Wilson, M. L. 2004. *C   * (Diptera: Culicidae) oviposition behavior determined by larval habitat quality and quantity in southeastern Michigan. – J. Med. Entomol. 41: 179–186.

Richmond, C. E. et al. 2007. Climate change and increased environmental variability: demographic responses in an estuarine harpacticoid copepod. – Ecol. Model. 209: 189–202.

Royama, T. 1992. Analytical population dynamics. – Chapman and Hall.

Schmid, P. E. 1992. Population-dynamics and resource utilization by larval Chironomidae (Diptera) in a backwater area of the River Danube. – Freshwater Biol. 28: 111–127.

Sæther, B. et al. 2000. Population dynamical consequences of climate change for a small temperate songbird. – Science 287: 854–856.

Spencer, M. et al. 2002. Oviposition habitat selection by mosquitoes (*C   *) and consequences for population size. – Ecology 83: 669–679.

Sun, Y. et al. 2007. How often will it rain? – J. Climate 20: 4801–4818.

Suttle, K. B. et al. 2007. Species interactions reverse grassland responses to changing climate. – Science 315: 640–642.

Tavecchia, G. et al. 2007. Density-dependent parameters and demographic equilibrium in open populations. – Oikos 116: 1481–1492.

Turner, J. T. et al. 2006. Zooplankton of Massachusetts Bay, USA, 1992–2003: relationships between the copepod *C   n   * and the North Atlantic Oscillation. – Mar. Ecol. Prog. Ser. 311: 115–124.

van de Pol, M. et al. 2010. E ects of climate change and variability on population dynamics in a long-lived shorebird. – Ecology 91: 1192–1204.

Visser, M. E. and Holleman, L. J. M. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. – Proc. R. Soc. B 268: 289–294.

Wilbur, H. M. 1987. Regulation of structure in compelx-systems – experimental temporary pond communities. – Ecology 68: 1437–1452.

Wilbur, H. M. and Fauth, J. E. 1990. Experimental aquatic food webs – interactions between 2 predators and 2 prey. – Am. Nat. 135: 176–204.

Yang, G. J. et al. 2008.Importance of endogenous feedback controlling the long-term abundance of tropical mosquito species. – Popul. Ecol. 50: 293–305.

Zedler, P. H. 2003. Vernal pools and the concept of "isolated wetlands". – Wetlands 23: 597–607.