



Quantifying the nature and strength of intraspecific density dependence in Arctic mosquitoes

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Abstract

Processes that change with density are inherent in all populations, yet quantifying density dependence with empirical data remains a challenge. This is especially true for animals recruiting in patchy landscapes because heterogeneity in habitat quality in combination with habitat choice can obscure patterns expected from density dependence. Mosquitoes (Diptera: Culicidae) typically experience strong density dependence when larvae compete for food, however, effects vary across species and contexts. If populations experience intense intraspecific density-dependent mortality then overcompensation can occur, where the number of survivors declines at high densities producing complex endogenous dynamics. To seek generalizations about density dependence in a widespread species of Arctic mosquito, *Aedes nigripes*, we combined a laboratory experiment, field observations, and modeling approaches. We evaluated alternative formulations of discrete population models and compared best-performing models from our lab study to larval densities from ponds in western Greenland. Survivorship curves from the lab were the best fit by a Hassell model with compensating density dependence (equivalent to a Beverton-Holt model) where peak recruitment ranged from 8 to 80 mosquitoes per liter depending on resource supply. In contrast, our field data did not show a signal of strong density dependence, suggesting that other processes such as predation may lower realized densities in nature, and that expected patterns may be obscured because larval abundance covaries with resources (cryptic density dependence). Our study emphasizes the importance of covariation between the environment, habitat choice, and density dependence in understanding population dynamics across landscapes, and demonstrates the value of pairing lab and field studies.

Keywords Resource competition · Hassell model · Beverton-Holt · Overcompensation · Mosquitoes · Arctic

Introduction

Processes that change as a function of density are inherent in all populations yet quantifying and sometimes even detecting these relationships remains a challenge (Strong 1986; Vickery and Nudds 1991; Rose et al. 2001). Arguably the most ubiquitous density-dependent process in nature is intraspecific resource competition, whereby increasing individuals of the same species decreases per-capita fitness due to limited resource supply (Nicholson and Bailey 1935). Since negative feedbacks from density dependence are necessary to produce population regulation, density dependence is at least implicit in most population models. Despite a rich body of theoretical work devoted to population models that incorporate processes that change with density (Ricker 1954; Beverton and Holt 1957; May et al. 1974; Hassell et al. 1976 and others), evidence for density dependence is often vague in empirical

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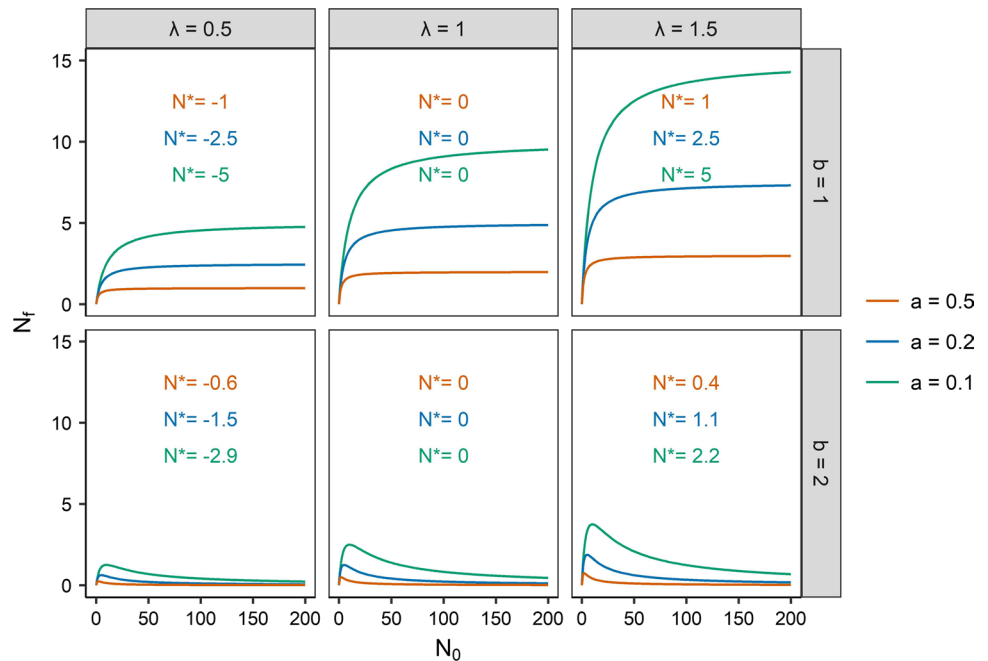
datasets, and its detection is sensitive to the nature of the data and the analytical methods employed (Dempster 1983; Strong 1986; Gaston and Lawton 1987; Hanski 1990; Woiwod and Hanski 1992). A variety of reasons have been proposed to explain this mismatch in theory and practice. Some authors suggest density dependence is challenging to detect in populations experiencing complex dynamics (Turchin 1990; Holyoak 1994), patch recruitment (Hassell 1987; Murdoch 1994; Wilson and Osenberg 2002; Shima and Osenberg 2003), and environmental stochasticity (Hassell 1987). Regardless of the reason, this highlights the need for studies that combine experimental and observational approaches to adequately characterize and quantify density-dependent processes in nature.

For organisms with discrete life stages, there is a long tradition of evaluating the strength of density-dependent processes by relating the density of individuals at one stage (e.g., breeders, N_0) to the number of individuals at a later stage (e.g., recruits, N_f). This is often done for populations across generations but can also be used to assess within-generation density-dependent effects. If the relationship between densities is linear such that the abundance of individuals at the subsequent life stage is proportional to the abundance at an earlier stage then density-dependent processes are assumed absent between stages (Quinn and Deriso 1999). If the relationship is curvilinear such that the population reaches a maximum, then either birth rates decrease with increasing density or death rates increase with increasing density, creating a negative feedback on population size that can produce a stable equilibrium. Density-dependent effects that are delayed or nonlinear can also push populations

towards complex endogenous dynamics, including cycles and even chaos (Turchin 2003).

Hassell’s discrete population model (1975) has useful characteristics for detecting the nature and strength of density-dependent processes. Similar to Beverton and Holt’s model (1957), the Hassel model contains one parameter for intrinsic population growth rate (λ) and another for the per-capita strength of intraspecific competition (a). Peak recruitment of the population increases with a higher population growth rate and lower per-capita competition (Fig. 1). The Hassel model also incorporates a density-dependent term (b) that changes the action of density dependence to reflect different modes of intraspecific competition (Hassell 1975; Anazawa 2019). When $b = 1$, the predicted density increases towards an asymptote representing the maximum recruitment (Fig. 1; Beverton and Holt 1957; Anazawa 2019). As b increases, the model produces a hump-shaped curve that displays overcompensation at high densities, where strong density-dependent mortality ‘overcorrects’ and decreases the number of survivors (Fig. 1; Ricker 1954; Anazawa 2019). The b term in the Hassell model can be interpreted as an index of resource inequality with $b = 1$ reflecting contest competition, where resources are monopolized by a few individuals, and $b \rightarrow \infty$ reflecting scramble competition, where resources are equitably spread but insufficient at high densities, producing overcompensation (Nicholson 1957; Anazawa 2019). A practical consequence of overcompensation is that adding an external source of mortality to a dense population at one life stage can ultimately act to increase population size. Some authors refer to this phenomenon as the hydra effect (Abrams and Matsuda 2005), while others

Fig. 1 Modeled relationships between initial (N_0) and final (N_f) densities of a given population based on Hassell (1975). Values of N^* are shown for different model parameterizations. The top row of panels depicts populations with compensatory dynamics ($b = 1$) and the bottom row depicts populations with overcompensatory dynamics ($b \geq 2$). Increasing finite net population change (λ) and decreasing per-capita competition (a) increases the peak recruitment (N_f) on the curves $N^* = \frac{\lambda^b - 1}{a}$



reserve that terminology for when unstructured consumer population exhibit cyclical dynamics (Schröder et al. 2014).

It remains an open question whether overcompensation is more of a theoretical curiosity that rarely manifests in nature, or whether there are some types of populations where it is relatively common. Stubbs (1977) suggested that most mammals and birds (K-selected organisms) display compensatory, and not overcompensatory density dependence. Clear examples include brown bears (Swenson et al. 1994), gray seals (Breed et al. 2013), and redhead ducks (Péron et al. 2012). Many empirical investigations of overcompensatory mortality are from organisms with complex life cycles (CLCs) with density-dependent processes acting strongly on the immature life stage (Vonesh and De la Cruz 2002; McIntire and Juliano 2018). Nicholson (1957) was among the first to demonstrate overcompensatory mortality in blowfly populations, where larvae “scramble” for food such that there were more emerging flies per unit quantity of larval food at lower densities compared to higher densities. Determining how and when exact compensation versus overcompensation might occur is commonly addressed in the study of fish populations dynamics because of its importance for fisheries management (Ricker 1954; Beverton and Holt 1957; Schmitt et al. 1999; Rose et al. 2001; Wilson and Osenberg 2002; Brannstrom and Sumpter 2005). The assumption that added mortality due to culling or harvesting will decrease the population size is incorrect for species at high densities with compensatory or overcompensatory response to external mortality (Cortez and Abrams 2016). Since overcompensation allows for populations to overshoot their carrying capacity, populations with overcompensating density dependence exhibit complex endogenous dynamics over time, ranging from damped oscillations to chaos (Barraquand et al. 2014). Thus, determining whether populations experience compensatory or overcompensatory dynamics is not only relevant for population control, but also for forecasting population size and dynamics over time.

Other organisms that can experience overcompensatory responses to external mortality are mosquitoes (Diptera: Culicidae) (Southwood et al. 1972; Washburn 1995; McIntire and Juliano 2018). As larvae, most mosquitoes consume microbes associated with decaying organic matter (Merritt et al. 1992) and populations experience density-dependent mortality and reduced growth from resource competition (Carpenter 1983; Livdahl and Sugihara 1984; Yee et al. 2007). A hydra effect was evident in the container breeding mosquito, *Aedes albopictus*, when mortality was introduced early in the life cycle (McIntire and Juliano 2018), which was consistent with the hypothesis that temporal separation between the added mortality and density-dependent mortality can produce hydra effects (Abrams 2009). Furthermore, several studies have shown that variation in larval habitat quality can influence the nature and strength of density

dependence across patches (Yee and Juliano 2006, 2012). Failing to account for heterogeneity in site quality could result in underestimating the strength of density dependence because the spatial ‘noise’ could obscure the temporal ‘signal’ of density dependence (Hassell 1987; Stewart-Oaten and Murdoch 1990; Shima and Osenberg 2003). Determining the species, habitats, and ecological contexts for which overcompensation is likely to occur remains a central question in mosquito ecology because of its importance for control efforts (Juliano 2007, 2009; Neale and Juliano 2019) and for anticipating pest and disease burden to humans and wildlife.

Here, we quantified within-generation mortality due to intraspecific resource competition in a common species of Arctic mosquito, *Aedes nigripes*, and assessed whether mortality resulted in undercompensation, compensation, or overcompensation (Fig. 1). Arctic mosquitoes were well-suited for this study because larvae display a long development period with few competitors, and intraspecific resource competition is a consequential driver of population dynamics (DeSiervo et al. 2020). Furthermore, larvae are amenable to lab studies (Culler et al. 2015) and populations are naturally found at a wide range of densities (< 1–> 100 larvae/L) across aquatic habitats (DeSiervo et al. 2020). Density-dependent mortality in the larval stage of *A. nigripes*’ life cycle is one of the strongest endogenous drivers of its population dynamics (DeSiervo et al. 2020) and is likely influenced by rapid changes in Arctic ecosystems including pond drying and resource availability (Finger Higgins et al. 2019). Determining whether populations experience compensating or overcompensating density dependence during the larval stage will improve predictive power about the extent of mosquito harassment experienced by humans and wildlife (Corbet and Downe 1966; Gaston et al. 2002; Witter et al. 2012; Joly et al. 2020) and the degree to which mosquitoes link aquatic and terrestrial systems as food for terrestrial predators (Wirta et al. 2015; Culler et al. 2021) and pollinators of Arctic plants (Urbanowicz et al. 2018).

To seek generalizations regarding the nature and strength of density-dependent processes in larval Arctic mosquito populations, we combined a laboratory experiment, field observations, and modeling approaches. First, we conducted a laboratory experiment where we manipulated larval densities and quantities of biofilm-coated detritus (food resources for larvae) and recorded the number of survivors. From those data we developed discrete population models, following Hassell (1975), to evaluate the nature of density dependence from intraspecific competition by contrasting competing models and interpreting parameters (Fig. 1). Next, we applied discrete population models to evaluate the nature of density dependence from intraspecific competition in field populations using four years of larval mosquito density data from ponds in western Greenland. These ponds vary

in their physical environment, nutrient loads, temperature, and the density of predators and competitors (DeSiervo et al. 2020). Previous work in this study system indicated a positive covariation between initial larval densities and food resources for larvae, suggesting that ovipositing females may lay more eggs in ponds with better food quality for larvae (DeSiervo et al. 2020). To evaluate whether this pattern holds across years and might obscure the detection of density dependence in this dataset, we evaluated if ponds with high and low densities of mosquitoes tended to stay consistent in rank order across years.

Materials and methods

Study system

Aedes nigripes (Diptera: Culicidae) is the most abundant and widespread Arctic mosquito species and the only species found near Kangerlussuaq, Greenland (67.009°N, 50.689°W), where we conducted field and lab work. Larvae of *A. nigripes* live in shallow snowmelt ponds and hatch within days of ice thaw (Corbet and Danks 1973; Dahl et al. 2004; Culler et al. 2015). The food source for developing larvae are biofilms composed primarily of bacteria and micro-algae that coat the surface of live and dead vegetation, usually *Carex* spp (DeSiervo et al. 2020, Supplemental video 1). Arctic mosquito larvae compete for food resources, experience mortality from predaceous diving beetles (*Colymbetes dolabratus*, Coleoptera: Dytiscidae) (Culler et al. 2015) and red-necked phalaropes (*Phalaropus lobatus*, Charadriiformes: Scolopacidae) and many die before emergence, especially when they are at high densities (DeSiervo et al. 2020).

Lab methods

We conducted a lab experiment to quantify density-dependent mortality in Arctic mosquito larvae and determine how this relationship might change with resource supply. We collected > 2000 early instar larvae (average individual dry mass = ~0.3 mg) from a pond not otherwise part of our study and allocated them to plastic cups that contained 0.15 L of coarsely filtered (1 mm) pond water and biofilm-coated detritus from the same pond. The experimental design was a 5×5 full factorial with six replicates per treatment combination (total $n = 150$, Supplemental Fig. 1). The density treatments were 1, 5, 10, 20, 40 larvae per cup (corresponding to ~7, 33, 67, 133, and 267 larvae/L) and 0, 1, 2.5, 5, 10 mg wet weight of biofilm-coated detritus (primarily *Carex* spp). The highest density treatment (244 larvae/L) was about double the maximum larval density observed in nature, and the food density

treatments visually matched conditions we observed in the field. All food treatments, including the 0 treatment, contained fine particulate organic matter (FPOM)—particles of 0.45–1000 μm coated in microbes that are food for developing larvae. Like other *Aedes* spp., Arctic mosquito larvae have a collector-gatherer feeding mode (Walker and Merritt 1991; Merritt et al. 1992), primarily feeding on biofilms on the surface of decaying vegetation (Supplemental Video 1), and also consuming FPOM that settles on the bottom of their aquatic habitats or mesocosms (M. D. personal observation).

We recorded the number of live mosquitoes every 3 days, removing dead individuals and exuviae and replenishing pond water with a small amount of FPOM as needed, but not adding additional biofilm-coated detritus. Although removing dead individuals and exuviae eliminates the recycling of resources within our experimental units, it was necessary for obtaining accurate counts. Furthermore, the rapid recycling of resources from dead individuals in cups was not likely to reflect conditions in natural aquatic habitats. Larvae were reared in environmental chambers at 9 °C and with 24 h of light (Danby Beverage Center DB039A1BDB) to mimic environmental conditions in the field. We compared the density of early instar larvae (N_0) to the density of surviving larvae at the end of the experiment (at 9 days, N_f).

Field methods

Larval densities were measured in a network of shallow mosquito ponds in 2011–2012 and 2017–2018 (Culler et al. 2015; DeSiervo et al. 2020). To quantify the density of mosquito larvae in ponds, we used a mosquito dipper (350 ml cup attached to a pole, Bioquip model 1132BQ) to collect five scoops of pond water every 8–10 paces in the littoral zone around each pond perimeter, starting when ponds thawed until no more pupae were found. Sampling took place during late May to June each year, and we visited each pond approximately every 4 days for density measurements, resulting in about six density measurements per pond per year during larval development. For statistical analyses and modelling purposes, we compared the number of early instar larvae/L (N_0 , defined as densities when individual larvae dry mass averages <0.2 mg) to the number of later instar larvae/L, N_f . This was the last density estimate for which we could assume that any previous decreases were due to mortality and not emergence. Of 22 cases where we had estimates of both N_0 and N_f from field populations, there were two cases where ponds shrank substantially over the season (> 60% decrease in pond size, DeSiervo et al. 2020), which artificially inflated final density estimates such that $N_f > N_0$. Those two ponds were excluded from further analyses.

Statistical analyses and modelling

To determine the nature and strength of density-dependent mortality across a wide range of densities and evaluate how this relationship might change with resource supply, we compared a series of models derived from Hassell (1975). The model (Eq. 1) had the form:

$$N_f = \frac{\lambda N_0}{(1 + aN_0)^b} \quad (1)$$

with N_f as the density of later instar mosquitoes (in L), N_0 as the density of early instar mosquitoes (in L), λ an estimated parameter representing the finite net rate of change (Hassell 1975), a an estimated parameter representing the per-capita strength of intraspecific competition, and b as tunable exponent representing the strength of density-dependent mortality, with $b = 1$ indicating exactly compensating density dependence (equivalent to a Beverton-Holt (1957) model). For this configuration of the model, when the finite net rate of change (λ) is ≥ 1 , increasing the per-capita strength of intraspecific competition (a) decreases the equilibrium (N^* , Fig. 1). We note that in our case, N^* represents the equilibrium density of late instar larvae within the same generation, and λ represents the net change in population growth between life stages, and thus both estimates are lower than they would be if we estimated them for the full life cycle where fecundity allows for population growth.

For our experiment data, we modified Eq. 1 to include variability in intraspecific competition (a) as a function of resource supply (F , Figure S1). To determine a suitable function for intraspecific competition (a) and food supply (F) within the Hassell model (Eq. 1) we compared a series of linear and nonlinear relationships between a and F and chose the model that maximized information content (AICc, Table S1). We expected a nonlinear, asymptotic relationship between the strength of competition and resource supply, where adding resources initially elicits a strong population response, which declines as satiation occurs. For all candidate models with different hypothetical relationships between a and F (Table S1), we solved for all parameters simultaneously (an intercept, λ , b , and a as function of F) using our lab experiment data ($n = 150$, 5 densities \times 5 food levels \times 6 replicates). Because our lowest food treatment consisted of 0 g of biofilm-coated detritus, but a small amount of FPOM, we added a scalar of 1.1 to all food treatment categories to avoid undefined numbers ($F' = F + 1.1$). The relationship between a and F' was well described with an inverse logarithmic function [$a = 1/(a_0 + a_1 \ln(F'))$, Supplemental Table 1) where the strength of intraspecific competition initially declined rapidly with additional food but leveled off at a higher

resource supply. We substituted this function for a into the Hassell model, resulting in the final model (Eq. 2):

$$N_f = \frac{\lambda N_0}{\left(1 + \frac{1}{a_0 + a_1 \ln(F')} N_0\right)^b} \quad (2)$$

with F' as the mass + 1.1 (in g) of food in our lab experiment (Figure S1), and parameters a_0 and a_1 fit to the data. For this configuration of the model with the reciprocal function in the denominator, it is important to note that increasing model parameters a_0 and a_1 decreases the per-capita strength of intraspecific competition, which increases peak recruitment (opposite of how a changes the functions in Fig. 1).

We then compared candidate models with different forms of intraspecific density dependence by varying parameter b . We compared models with no density dependence, where $b = 0$ (with and without a density \times food interaction, models 0–3 in Table 1), exactly compensating density dependence, where $b = 1$ (model 4 in Table 1), and models where b could vary such that $0 < b < 1$ represents undercompensation, and $b > 2$ represents overcompensation (models 5 and 6 in Table 1). Parameters for all models were first estimated by minimizing the residual sum of squares using the (solver) function in Excel. We used these as starting values for parameter estimates with the nls function in R, and allowed the models to converge (package nls, R Core Team 2019). After identifying the candidate model that maximized information content, we interpreted model parameters to infer the nature and strength of density dependence in the lab experiment. Parameter b was interpreted as an indicator of compensatory dynamics, and parameters λ and a (now a_0 and a_1) were used to assess peak recruitment in the presence of intraspecific competition (Fig. 1).

For the field estimates of population densities, we ran two sets of analyses. To test if ponds with initially high and low densities of mosquitoes (N_0) tended to stay consistent across years we ran two-way ANOVAs with type III sum of squares that included site, year, and site \times year (package car, R Core Team 2019). Since we did not have a complete set of densities from all ponds in all years we ran this model on three subsets of the data, comparing the density of four ponds sampled in 2011 and 2012, three ponds sampled in 2017 and 2018, and two ponds that were sampled in all four years. Field density data were first normalized with $a \ln + 1$ transformation. To test the nature and strength of intraspecific density dependence using the field data, we compared the fit of Hassell models derived after Eq. 1 with varying values for b . Again, we interpreted estimated model parameters to draw inferences regarding the nature and strength of density dependence in field populations.

Table 1 Parameter estimates and AIC output of competing models representing different modes of intraspecific competition in *Aedes nigripes* from the laboratory study ($N=150$)

Models	Parameter estimates (± 1 SE)							RSS	No. parameters	Δ AIC
	β_0	λ	β_2	β_3	a_0	a_1	b			
0 No dd, $b=0$, intercept only ^a	3.82 ± 0.26							1468	1	205
1 No dd, $b=0$, no intercept ^b		0.11 ± 0.01	0.43 ± 0.03					710	2	98
2 No dd, $b=0^c$	-0.07 ± 0.36	0.11 ± 0.01	0.44 ± 0.05					709	3	101
3 No dd, $b=0$, interaction ^d	1.13 ± 0.41	0.04 ± 0.02	0.19 ± 0.07	0.02 ± 0.003				610	4	80
4 Compensation, $b=1^e$		1.29 ± 0.17			0.63 ± 0.28	3.70 ± 0.74	1	363	4	0
5 Variable, $b > 0^e$		1.25 ± 0.26			0.76 ± 0.74	4.20 ± 2.47	1.04 ± 0.21	362	5	2
6 Overcompensation, $b > 2^e$		0.93 ± 0.12			5.11 ± 4.3	15.63 ± 9.82	2.00 ± 0.78	384	5	11

Models are listed by the number of parameters (*dd* density dependence)

Parameter estimates are represented ± 1 SE

RSS represents the residual sum of squares of each model and the difference between AIC and the lowest-ranked model (model 4, compensation) is shown in the right column

^a $N_f = \beta_0$

^b $N_f = \lambda(N_0) + \beta_2(F)$

^c $N_f = \beta_0 + \lambda(N_0) + \beta_2(F)$

^d $N_f = \beta_0 + \lambda(N_0) + \beta_2(F) + \beta_3(N_0 \times F)$

^eEq. 2

Results

In the lab, survivorship was highest for mosquitoes in experimental treatments with the lowest densities (N_0) and highest food supplies (F') (Fig. 2). The model with compensatory density dependence ($b=1$) was the best fit for the lab data (Table 1, Fig. 2B), suggesting contest competition for resources amongst *A. nigripes* larvae. Additionally, for the model where we allowed b to vary, the parameter converged on an estimate very close to 1 (1.04 ± 0.20 , Table 1). In contrast, the linear models ($b=0$), and the model allowing for overcompensation ($b > 2$), were poorer fits to the data (Table 1). The predicted range of maximum survivors (asymptotes for the Hassel model with $b=1$) were 8–81 mosquitoes/L depending on resource availability (Fig. 2B).

For field populations that we sampled in multiple years (Table S2), early instar densities varied tenfold across sites and years from < 1 larva to > 100 larvae/L and ponds with relatively high and low densities of mosquitoes remained consistent across years (Fig. 3, Table S3). Pond 2 had the highest densities in 2011 and 2012, but this pond dried and could no longer be sampled in subsequent years (Fig. 3). Pond 4, which was sampled in all four years, consistently had the lowest density of larvae (Fig. 3). Overall, mosquito larval densities were highest in 2018, and lowest in 2012 (Figs. 3, 4). Only two of 20 ponds, both from 2018, had average initial instar densities greater than 50 mosquito larvae/L (Fig. 4).

Two of our discrete population models performed about equally well for the field data (Table 2), although all models had relatively large residual error compared to the models for the laboratory data, which also included measurements of resource supply (Table 1). The linear model without an intercept ($b=0$) had the lowest AIC, followed very closely by the compensation model ($b=1$) (Table 2). The estimated parameter for a in the model with compensatory density dependence overlapped zero (Table 2). The overcompensation model ($b > 2$) was a poor fit for the data (Table 2). The asymptote for the Hassel model with compensatory density dependence ($b=1$) was 49 mosquitoes/L (peak value = λ/a when $b=1$, Figure S2). This approximated the peak value as determined by our lab experiment with a resource supply of 1 g biofilm-coated detritus/150 mL (Fig. 2B). Almost all the initial larval densities from the field were less than this maximum predicted value of 49 mosquitoes/L, falling within the approximately linear portions of the nonlinear survivorship functions (Fig. 4).

Discussion

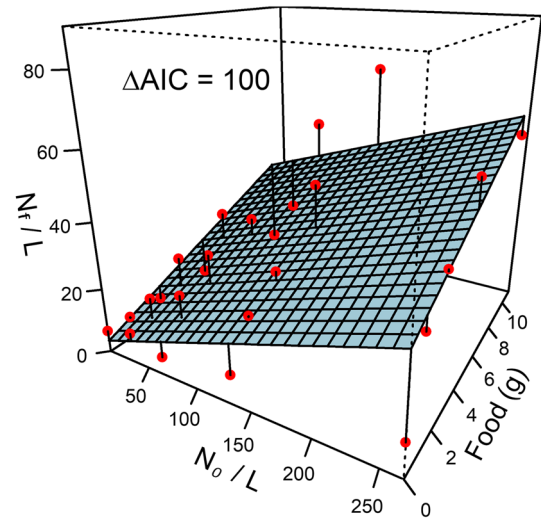
Our lab data showed evidence for density dependence and favored the hypothesis that mortality is generally compensatory in the larval stage of *A. nigripes* with variability in

Fig. 2 The final densities of surviving *Aedes nigripes* larvae (N_f per L pond water) as a function of the initial density of early instars (N_0 per L pond water) and the amount of biofilm-coated detritus (Food, in g wet mass, F). Points represent the average number of surviving larvae after 9 days for each density \times food treatment ($N=150$). Blue surfaces in a-c represent the model fits for 2, 4, and 6, respectively (described in Table 1). The model in **a** did not include density-dependent mortality and was a poor fit to the data. The model in **b** with compensatory density dependence, performed better than the model in **c** with overcompensating density dependence. Note that the blue surface in **c** only barely reaches a maximum value before it turns over within this range of densities

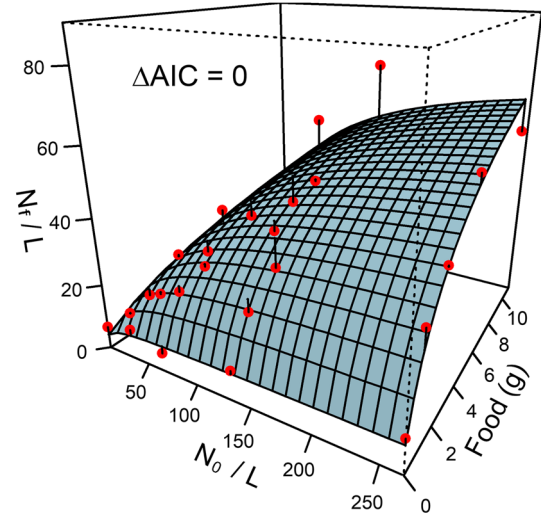
peak recruitment depending on food supply (Table 1, Fig. 2). This suggests that contest competition for larval resources (biofilm) is a better match than scramble competition for resources in Arctic mosquito larvae. In contrast to our laboratory study, our measurements of density in the field did not show a signal of strong density dependence (Fig. 4, Figure S2). We do not think this was an artifact of low statistical power because the average density varied among ponds by almost an order of magnitude (and several standard errors, Fig. 3). Rather we think it was because (1) the ponds were of variable quality for mosquito fitness and (2) larval density was highest in the ponds that would have otherwise been of the best quality for mosquito development (DeSiervo et al. 2020). Higher densities in high-quality patches compared to low-quality patches can obscure the signal of density dependence in organisms with discrete life cycles. Had we only seen the field data (Fig. 4), we might have concluded that density dependence from the intraspecific competition is relatively weak for *A. nigripes* in Greenland. Thus, our study highlights the benefit of using multiple approaches to investigate density-dependent processes, and adds to the case that considering covariation between the environment, habitat choice, and density dependence is important when populations vary in space and time (Hassell 1987; Shima and Osenberg 2003; Briggs and Osenberg 2019).

Determining the strength and form of density dependence is fundamentally important to the dynamics of any population. Collectively, our results suggest a point equilibrium for *A. nigripes* rather than more complex endogenous dynamics such as limit cycles or chaos. *Aedes nigripes* populations in Greenland may fluctuate by orders of magnitude in back-to-back years (Fig. 3), but this is apparently not a product of complex dynamics produced by intraspecific density dependence. A more probable explanation for large interannual variation in total population size is that the point equilibrium is noisy because of environmental stochasticity. Interannual variation in climate, a hallmark of Arctic ecosystems (Post et al. 2019), changes the size and extent of aquatic habitats in our study area, which subsequently determines the number of larvae that hatch annually. Previous research in this system demonstrated that per-capita mortality was the most important contributor to estimated population

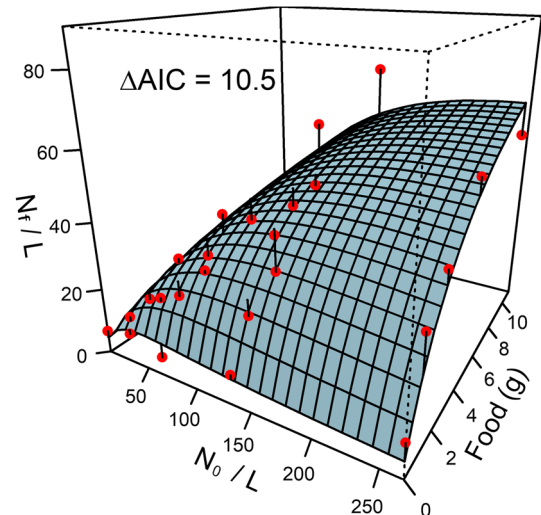
(a) No DD, $b = 0$



(b) Compensation, $b = 1$



(c) Overcompensation, $b = 2$



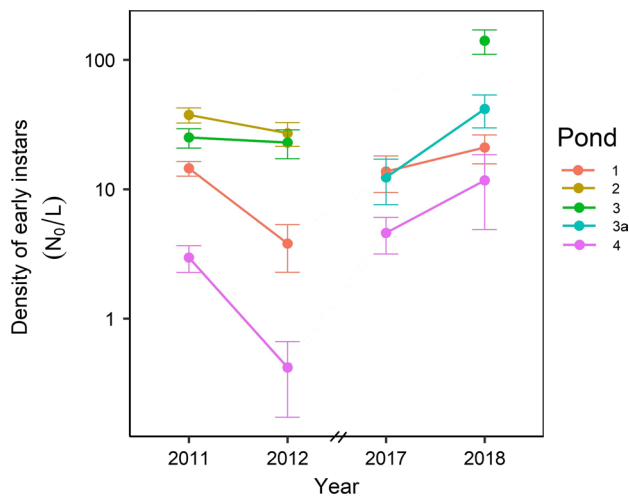


Fig. 3 The density of early instar mosquito larvae (per L) across five ponds with at least two years of sampling ($N=15$ ponds). Densities varied among ponds and years, but ponds with relatively high and low densities remained consistent in rank order across years. Points represent average densities of *Aedes nigripes* from 10 to 40 scoop samples around the littoral edges of ponds ± 1 SE. Lines are drawn between density samples in back-to-back years

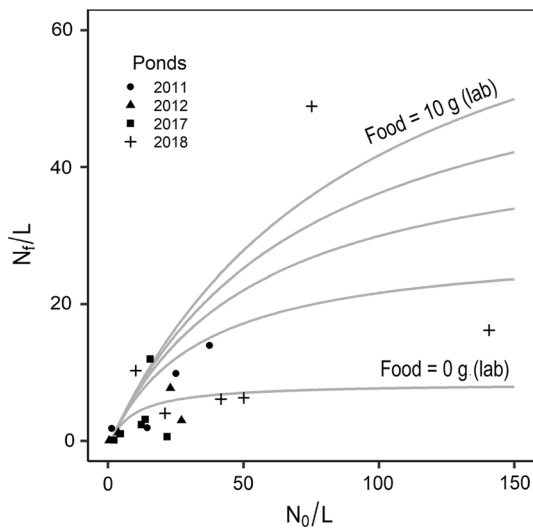


Fig. 4 The initial number of *Aedes nigripes* larvae per liter (N_0 , per L pond water) versus the final number of larvae per liter just before emergence (N_f , per L pond water) across ponds sampled during 2011–2018. Symbols denote the year of sampling ($N=20$). Curves represent the best models for each of the five food treatments (F) in the lab experiment (Fig. 2B) overlaid on the field data. Allowing for a range of food availabilities (gray functions derived from the lab experiment) easily encompassed the range of our measurements in natural ponds (the points). This demonstrates how environmental variation (in this case, resource variability) could contribute to variation in recruitment functions, making density dependence difficult to detect using field density data alone

growth between generations (DeSiervo et al. 2020), providing confidence in our assessment of equilibrium stability.

Nonetheless, we exercise caution in interpreting the raw values of N^* and λ from this study, since they were estimated using only part of the life cycle. More research is needed to integrate estimations of larval mortality with demographic parameters at the adult stage, for example, success in finding a blood meal (see Culler et al. 2018) to accurately predict total population equilibrium and population growth rate. Furthermore, future research on the density and abundance of hatching larvae in Arctic ponds as a function of the environment (for example pond size) would complement the biotic mechanisms that we explored in this lab and field study and would increase our ability to predict the extent of mosquito harassment experienced by humans and wildlife.

Our data and interpretations emphasize the importance of density dependence during the larval life stage of *A. nigripes*. This is in accord with what has been generally reported for mosquitoes and other taxa with complex life cycles (e.g., Juliano 2007). We do not reject the possibility of density-dependent effects at other life stages, perhaps during eclosion or acquisition of blood meals by female adults, but these seem likely to be small compared to intense density-dependent mortality during the larval stage. Additionally, our study focused on survivorship and we did not account for density-dependent effects on female size at eclosion, an important component of other studies in mosquito ecology (Neale and Juliano 2020). Previous research in this system demonstrated that daily mortality rate during the larval stage was by far the strongest direct contributor to variation among ponds in population growth (74%), while female size at eclosion, an indicator of potential fecundity, contributed far less (17%) (DeSiervo et al. 2020).

Although many studies have shown strong density-dependent mortality in larval mosquito populations (Livdahl 1982; Renshaw et al. 1993; Leonard and Juliano 1995; Gimnig et al. 2002) only a few have addressed the theoretical possibility of overcompensation (Southwood et al. 1972; McIntire and Juliano 2018; Neale and Juliano 2019). Two scenarios that could produce hydra effects in mosquitoes are (1) larval populations display strong density-dependent mortality due to food limitation that lead to a temporal separation between density-dependent mortality and added mortality and (2) non-lethal behavior shifts from the presence of predators that results in more limited resource exploitation (Abrams 2009; McIntire and Juliano 2018). Our experimental protocol enhanced the likelihood of detecting overcompensation because we removed dead individuals and exuviae and, therefore, reduced the recycling of resources for remaining survivors. Thus, although *A. nigripes* seemed like a good candidate for overcompensatory density dependence (large interannual fluctuations in population size, long larval development time, few interspecific competitors), our results indicated that overcompensation rarely or never occurs in our study system.

Table 2 Parameter estimates and AIC output of competing models representing different modes of intraspecific competition in *Aedes nigripes* from field density data collected over four years of study (Supplemental Table 1, $N=20$)

Models	Parameter estimates (± 1 SE)				RSS	No. parameters	Δ AIC
	β_0	λ	b	a			
No dd, $b=0$, intercept only ^a	7.15 \pm 2.43				2247	1	7.85
No dd, $b=0$, no intercept ^b		0.23 \pm 0.05			1517	1	0.00
No dd, $b=0^c$	2.17 \pm 2.65	0.20 \pm 0.06			1462	2	2.06
Compensation, $b=1^d$		0.42 \pm 0.2	1	0.009 \pm 0.011	1320	3	0.01
Overcompensation, $b>2^d$		0.50 \pm 0.40	5.0 \pm 100	0.002 \pm 0.040	1279	4	2.55

Models are listed by the number of parameters (dd density dependence)

Parameter estimates are represented ± 1 SE

RSS represents the residual sum of squares of each model and the difference between AIC and the lowest ranked model (model 1, no dd) is shown in the right column

^a $N_f = \beta_0$

^b $N_f = \lambda(N_0)$

^c $N_f = \beta_0 + \lambda(N_0)$

^dEq. 1

One factor that could contribute to whether mosquito populations experience compensatory or overcompensatory dynamics is larval feeding mode. Feeding mode in nonpredator larval culicids varies widely across species and contexts, and includes filter-feeding particulate matter from the water column, collecting and gathering particles on surfaces, scraping, and shredding (Merritt et al. 1992). *Aedes nigripes* mosquito larvae have a collector-gatherer feeding-mode (Walker and Merritt 1991; Merritt et al. 1992), using their lateral palatal brushes to push loosely attached particles from a surface into their mouths (Supplemental Video 1). The dispersion of resources (random, clumped, or uniform) could influence the form of competition in the consumer. When resources are aggregated, for example, on a surface, larvae are more likely to interfere with one another in gaining access to the food resource, resulting in a contest competition (compensation) outcome, where some larvae gain more resources than others. In contrast, species that filter-feed may be more likely to experience scramble competition (overcompensation) because there is a more equitable spread of resources, resulting in widespread mortality when consumers are at high densities because the resource supply is insufficient. Future studies on density dependence in mosquito larvae might benefit from comparing how species with predominantly filter-feeding behavior (including most *Anopheles* and many *Culex* species) differ from those that consume biofilm or periphyton (most *Aedes* species) in how resource competition manifests and changes the action of density dependence within populations.

A central, yet counterintuitive aspect of our study was that we found conclusive evidence for density dependence in Arctic mosquito larvae from the laboratory study, but

little evidence for density dependence with the field data. We propose a few nonexclusive possibilities for the apparent mismatch between lab and field studies. The first is simply an issue of the span of population densities we observe in nature. From the laboratory experiment, we determined that recruitment functions were approximately linear up until a density of 40 early instar larvae/L for a resource supply of ≥ 1 g of biofilm-coated detritus/150 mL (gray lines in Fig. 4). In fact, most of the populations we observed in nature were less than 40 early instar larvae/L, thus we would not expect to observe much density-dependent mortality in these populations. From a population control perspective, this implies that adding an extrinsic source of mortality to most larval populations of *A. nigripes*, for example a larvicide, would be effective at reducing population density. As Chesson and Huntly (1997) point out, low population densities do not necessarily imply that competition does not have appreciable effects on population and community dynamics, but rather that multiple mechanisms are involved. It seems likely that in this system, other processes such as predation or egg-mortality, could play an important role in lowering *A. nigripes* larval densities in certain years to the point where little or no intraspecific competition occurs. The ponds in our study system vary conspicuously in densities of the prominent larval predators – predaceous diving beetles (Culler et al. 2015; DeSiervo et al. 2020) and red-necked phalaropes. Experimental investigations of interactions between predators and resource competition would be possible by adding a factor for predator density to studies such as we report here.

Another likely explanation for why we did not observe the temporal signal of density dependence in field populations

of *A. nigripes* is a phenomenon known as cryptic density dependence (sensu Wilson and Osenberg 2002). Cryptic density dependence can emerge in studies when site quality is confounded with habitat selection, such that more individuals end up in better sites, making density dependence difficult to detect with field sampling and traditional analytical methods without explicit knowledge of variation in habitat quality (Fig. 4). In their studies of coral reef fish, Shima and Osenberg (2003) found no evidence for density dependence when they examined a large dataset comparing the density of settler fish to the predicted density of surviving fish; however, density dependence emerged as Beverton-Holt functions when they binned sites by environmental quality. Our lab experiments with *A. nigripes* indicated compensatory density-dependent mortality, with the density-dependent function being itself a function of the environment (resource quantity in this case, Table 1, Table S1, Figure S1). This model might be consistent with our measurements of densities and survival in nature if we allow for variable food resources across ponds (Fig. 4).

Spatial covariation between environmental quality and population density can occur via both passive mechanisms (e.g., low dispersal out of good patches), and active mechanisms (e.g., habitat searching and habitat selection). In our study system, ponds with better food resources tended to have more hatching mosquitoes (DeSiervo et al. 2020), matching one of the important criteria for cryptic density dependence (Shima and Osenberg 2003). Furthermore, our multi-year analysis of densities across pond revealed that high and low-density ponds tend to stay consistent across years (Fig. 3). The mechanism that maintains co-variation between immature population density and environmental quality remains unknown for this system. One possibility is that adult female dispersal is low enough that ponds with more emerging adults also tend to also have more ovipositing females. Another possibility is that ovipositing females are more likely to find or remain near ponds with good larval resources. Availability of blood meals for adult mosquitoes seems another likely explanation for aggregation in ovipositing adults (Culler et al. 2018), but it is not clear how this would promote more oviposition in ponds that have better food for larvae.

Our study emphasizes the value of pairing lab and field studies to gain a mechanistic understanding of what governs fluctuations in the abundance of natural populations. Laboratory studies are beneficial because they allow researchers to isolate one or a few variables that could be important in governing population dynamics while keeping others constant. Lab studies also allow for the observation of biological processes across a wide gradient of conditions (densities and food supply in this case) even if some combinations are unlikely to occur in nature. Broad gradients in experimental

studies are particularly helpful for determining nonlinear effects, which are common in population demography studies.

Our technical approach for studying density dependence could be applicable to other systems in the Arctic and elsewhere. It is particularly relevant to systems that include strong environmental gradients and management interests in population control, sustainable harvesting, or conservation. Knowledge of recruitment relative to initial abundance has practical value because it determines the range over which external mortality (e.g., from a larvicide, predator, or environmental perturbation) would or would not reduce population size (Juliano 2007; Cortez and Abrams 2016). We modified Hassell models such that peak recruitment values increased nonlinearly with food supply. One could similarly consider the effects of food quality, temperature, and other factors on the form of density dependence.

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Author contribution statement MHD conceived and designed the experiments, collected, and analyzed the data, and wrote the manuscript. LEC assisted in experimental design, collected data, and edited the manuscript. MPA assisted in project design, data analysis and edited the manuscript. All authors gave final approval for publication.

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Data availability material The datasets and the code used for statistical analyses in the current study are available from the corresponding author on reasonable request.

Declarations

Conflicts of interest The authors declare no conflicts of interests.

Ethical approval Ethics approval was not required for this study according to local legislation (Naalakkersuisut, the Government of Greenland).

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