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Spatial heterogeneity in the abundance and fecundity of Arctic mosquitoes

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Abstract. The abundance of mosquitoes is strongly influenced by biotic and abiotic factors that act on the immature (aquatic) and adult (terrestrial) life stages. Rapid changes in land use and climate, which impact aquatic and terrestrial mosquito habitat, necessitate studying the ecological mechanisms, and their interplay with the changing environment, that affect mosquito abundance. These data are crucial for anticipating how environmental change will impact their roles as pests, disease vectors, and in food webs. We studied a population of Arctic mosquitoes (*Aedes nigripes*, Diptera: Culicidae) in western Greenland, a region experiencing rapid environmental change, to quantify spatial variation in adult abundance and reproduction. Using sweep nets, we collected about sevenfold more mosquitoes within the town of Kangerlussuaq and within a low-elevation tundra valley compared to three other tundra locations. Dissections of adult female mosquitoes revealed that only 17% were gravid overall, with a range of 7–43% among sites. If gravid, mosquitoes matured an average of 60 eggs per individual—more in larger females. We found no indication of autogenous egg development. Analyses using our field data indicated that spatial variation in adult fecundity and survival of immatures could each account for a 10-fold range in the per capita growth of mosquito populations. The availability of vertebrate hosts and aquatic habitat is changing in many parts of the Arctic and can be expected to influence Arctic mosquito abundance. In the Arctic, and elsewhere, life-history data from natural populations of mosquitoes will significantly aid in understanding controls on the abundance of these globally ubiquitous insects.

Key words: Arctic; mosquitoes; population change; tundra; vertebrate hosts.

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INTRODUCTION

Mosquitoes (Diptera: Culicidae) are a diverse and globally ubiquitous clade of insects that transmit significant human disease and are important to the structure and functioning of many ecosystems (e.g., Fang 2010, Shragai et al. 2017). In aquatic environments, immatures (larvae and pupae) are food for invertebrates (e.g., Culler and Lamp 2009), fish (e.g., Louca et al. 2009), and birds (Pielou 1994). Adults in terrestrial

ecosystems are prey for lizards (Canyon and Hii 1997), spiders (e.g., Dabrowza-Prot et al. 1968), bats (e.g., Weterings et al. 2017), and birds (Jedlicka et al. 2017). Adult females are also parasites of vertebrates. Their blood-seeking behavior can be a major factor in the movements, behavior, abundance, and physiological condition of animal populations (e.g., Day and Edman 1984, Helle and Tarvainen 1984, Witter et al. 2012). Despite the global relevance of mosquitoes to humans and natural systems, data on basic mosquito

ecology are often outdated or lacking. Thus, it remains a challenge to understand the ecological mechanisms, and their interplay with the changing environment, that act on the immature and adult stages to determine abundance (Chaves 2017, Shragai et al. 2017).

The complex life cycle of mosquitoes makes them particularly sensitive to environmental change (Ewing et al. 2015, Shragai et al. 2017). Factors acting on both the immature and adult stages can influence mosquito population dynamics and abundance (e.g., Chaves et al. 2014). Pond drying, predation, exposure to high temperatures, water quality, and resource competition during the larval stage can lead to mortality before emergence (Bar-Zeev 1958, Walker et al. 1997, Strand et al. 1999, Culler et al. 2015) and reduced adult size (Agnew et al. 2000, Chaves et al. 2011, Walsh et al. 2011). This impacts fecundity because smaller females lay fewer eggs (Briegel 1990). Of mosquitoes that survive to the adult stage, reproduction is dependent on successful mating, and, typically, adult females procuring a blood meal and finding suitable habitat for oviposition (Day et al. 1990, Edman et al. 1998). If blood meals are scarce near otherwise suitable habitat, mosquito abundance may be limited by adult reproductive success vs. density-dependent factors acting on the immature stages, which are often limiting processes for mosquitoes (e.g., Hoshi et al. 2017, Chaves and Moji 2018). However, for some species, the ability to produce eggs autogenously presumably eases the dependence of mosquito abundance on vertebrate host availability (Corbet 1964, 1967, Spielman 1971).

Climate and land use change can influence both the terrestrial and aquatic habitats utilized by mosquitoes. Aquatic habitats are subject to changes in temperature and precipitation, the evaporative balance of which determines aquatic habitat duration, stability, and the extent of crowding, which can impact immature mortality (Sota et al. 1994, Rosà et al. 2014, Marini et al. 2016) and adult size (Chaves et al. 2011, Mulatti et al. 2014). Furthermore, temperature dictates mosquito growth rates and stage-specific phenology (Chaves et al. 2018), which can impact immature survival (Loetti et al. 2011, Ciota et al. 2014, Culler et al. 2015) and adult size (Lyimo et al. 1992, Christiansen-Jucht et al. 2015). In the

terrestrial environment, adult mosquito longevity (Shapiro et al. 2017), reproduction (Reisen et al. 2010), and abundance (Hoshi et al. 2017) are influenced by temperature. In the absence of autogeny, reproduction may be further impacted by the availability of vertebrate hosts (Wekesa et al. 1996). The local abundance of vertebrate hosts can be influenced by land use practices and species-specific responses to climate change (e.g., range shifts; Hickling et al. 2006).

We studied a natural population of mosquitoes in the Arctic to explore the ecological mechanisms that determine abundance, with a focus on spatial variability and adult reproduction. We collected adult mosquitoes from multiple locations in West Greenland tundra, measured size distributions, and dissected the abdomens of female mosquitoes to determine the proportion that were gravid and the number of eggs per gravid female. Our data permitted (1) estimating variability in abundance and fecundity across the landscape, (2) evaluating the contributions to mosquito populations from autogenous reproduction, which was previously described for this species in another Arctic location (Corbet 1964, 1967), and (3) characterizing the relationship between adult size (a function of larval habitat) and fecundity. Collectively, the data allowed us to estimate spatial heterogeneity in population growth rates, that is, how many adult female mosquitoes in generation $t + 1$ are produced by an average female in generation t , under a variety of scenarios representing spatial variability in adult reproduction and survival of immature mosquitoes in Arctic ponds, which was previously found to be sensitive to temperature (Culler et al. 2015). Although species diversity of Arctic mosquitoes can be low, high abundances of the species that are present (Jenkins 1958) enable their role as pests (Helle and Tarvainen 1984, Gaston et al. 2002, Hagemoen and Reimers 2002, Witter et al. 2012), in food webs (Fang 2010, Koltz et al. 2017), and sometimes even as pollinators (Urbanowicz et al. 2017).

METHODS

Study system

We conducted our study near Kangerlussuaq, Greenland (Fig. 1), a small town adjacent to the Greenland Ice Sheet (2016 population = 499).

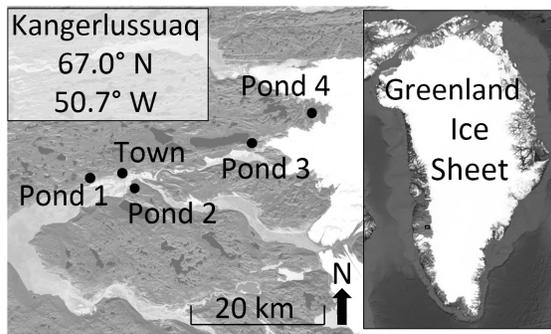


Fig. 1. Points represent the five study sites near Kangerlussuaq, Greenland (Town). Map data: Google Earth, Image 2018 DigitalGlobe.

About 15% of landscape is covered by freshwater lakes and ponds within a matrix of tundra vegetation dominated by shrubs and graminoids (Heindel et al. 2015). The only mosquito species in our study area is *Aedes nigripes* Zett. (Diptera: Culicidae, Kalaallisut: ippernaq), the most widely distributed mosquito species in the Arctic (Jenkins 1958). Immature *A. nigripes* hatch from eggs and develop in shallow temporary ponds during May and June (Culler et al. 2015). After adult emergence, which typically begins in late May or early June, females mate and seek a blood meal. In June and July, matured eggs are laid in the drying margins of ponds that will become wetted larval habitat during the following spring (Corbet and Danks 1973). In one high-Arctic location, females of this species were able to mature eggs autogenously, that is, without a blood meal (Corbet 1964, 1967). As larvae and pupae, mosquitoes are prey for the predaceous diving beetle *Colymbetes dolabratus* (Coleoptera: Dytiscidae) and also Red-necked Phalaropes that occur on some mosquito ponds (L. E. Culler, *personal observation*). Similar to other mosquito species in small ponds, predation acts heavily on the immature stage (Service 1993), but spiders likely exert additional predation pressure during and after emergence (L. E. Culler, *personal observations*).

Although this species may have the potential to mature eggs autogenously (Corbet 1964, 1967), in which case larval nutrition would be important control on fecundity (Spielman 1971), the availability of vertebrate hosts (for blood meals) in Kangerlussuaq was expected to be variable across the landscape. A migratory herd of

caribou (*Rangifer tarandus*) utilizes a valley in the Kangerlussuaq area, arriving from the coast each year just before giving birth to calves (average date of 5 June with little interannual variability [Post and Forchhammer 2008]). Muskox (*Ovibos moschatus*), Arctic hare (*Lepus arcticus*), and Arctic fox (*Vulpes lagopus*) are also present, although patchy and less common than caribou (L. E. Culler, M. P. Ayres, and R. A. Virginia, *personal observation*). Migratory birds including Wheatears, Redpolls, Lapland Longspurs, and Canada Goose are relatively common throughout the landscape (M. P. Ayres, *personal observation*). During summer, a few hundred tourists and travelers arrive and depart most days from Europe and other locations in Greenland, which does not quite double the local population size of Kangerlussuaq during the daytime hours.

After mosquitoes began to emerge in early June of 2012 (first emergence in 2012—1 June; Culler et al. 2015), we sampled adults from the margins of four mosquito ponds and an additional site in the town of Kangerlussuaq (Fig. 1). We visited each site during the afternoon hours (13:00–16:00 local time) on 12, 18, and 25 June and collected adult mosquitoes that were resting on vegetation using sweep nets. Due to the distance among our sites, Pond 3 and Pond 4 were sampled first on each sampling date, with the remaining three sites sampled randomly thereafter (Pond 1, Pond 2, and Town). We collected six 60-sweep samples (approximately 60 s per sample) at each site on each date. The six 60-sweep samples were collected haphazardly at each site, always with the same two researchers collecting three samples each. A sweep net (diameter = 30 cm) was dragged back and forth 60 times through shrub and grass vegetation while walking a transect of 25 m that was haphazardly located within the much larger matrix of similar habitat. After 60 sweeps and 25 m, the sample was transferred to a bag and chilled on ice until adult mosquitoes were counted and preserved in 70% EtOH. Later, each adult female was dissected under a dissecting microscope to determine whether she was gravid and to count the number of eggs in her abdomen. We also measured wing length as an indicator of body size, which was subsequently converted to dry mass (mg) using a dry mass to wing length regression developed for Kangerlussuaq mosquitoes (Appendix S1: Fig. S1).

Analyses

We tested how sampling site and date affected the number of mosquitoes collected using analysis of variance (proc glm, SAS v. 9.4, SAS Institute, Cary, North Carolina, USA). Count data were transformed as $\ln(x + 1)$ prior to analysis to meet normality assumptions. We then tested how the proportion of gravid females varied among sites and dates using binomial regression (proc glm, SAS v. 9.4).

To further analyze the proportion gravid and the egg count per female mosquito, we plotted distributions of egg numbers and compared the goodness of fit of alternative frequency distributions via maximum-likelihood estimation (AIC) with the R package pscl (Jackman 2008). Candidate distributions included (A) Poisson; (B) negative binomial; (C) zero-inflated Poisson; and (D) zero-inflated negative binomial (ZINB). All describe a discrete count distribution, and models C and D add an additional parameter to allow for a surplus of zero counts relative to their simpler analogues. Because it was strongly favored in the model comparisons (Appendix S1: Table S1), we used the ZINB model (Zeileis et al. 2008) to compare proportions and egg numbers among sites. The three-parameter model describes the probability that a female mosquito was not gravid (zero-inflated component, ϕ) and the frequency distribution of eggs for those that were gravid (mean, λ ; variance, θ). We estimated and compared parameters of ZINB regression models with the R package pscl (Jackman 2008, Zeileis et al. 2008). We then fit a linear regression model to test whether body size explained residual variation in the number of eggs per gravid female (proc glm, SAS v. 9.4).

Population model

We used our field measurements to estimate population replacement rate, R , for mosquitoes at each site, that is, the average number of adult females in generation $t + 1$ produced by an average female in generation t , where:

$$R = \text{probability}(\text{gravid}) \times (\#\text{eggs}|\text{gravid}) \times \text{probability}(\text{adult}_{t+1}|\text{egg}) \quad (1)$$

We estimated $\text{probability}(\text{gravid})$ for each site from the ZINB model as $1 - \phi$ (the zero-inflated component) and $\#\text{eggs}|\text{gravid}$ was estimated as λ

(from the ZINB model) $\times 0.5$, assuming a 50:50 sex ratio of mosquito eggs (but see *Results*) and because our population model only accounted for females. We varied $\text{probability}(\text{adult}_{t+1}|\text{egg})$ from 0 to 1 to account for variation in survival rates from the egg through the adult stage. Our previous study indicated immature survival probabilities ranging from 0.01 to 0.40 among ponds in 2011 and 2012 (Appendix S1: Table S2; Culler et al. 2015). We also assumed that females could only complete one gonotrophic cycle, that is, mature and oviposit eggs after a blood meal only once. Other studies have found this to be true for univoltine, northern *Aedes* species (Carpenter and Nielsen 1965), which die shortly after the first oviposition (Nielsen 1959).

RESULTS

We collected a total of 3545 mosquitoes, and all were female (Table 1). The number of mosquitoes collected varied greatly among sites ($F_{4,83} = 44.0$, $P < 0.0001$) but not among dates ($F_{4,83} = 1.2$, $P = 0.32$; Fig. 2). We collected the most mosquitoes at Pond 3 and Town, which had more mosquitoes than Pond 1, Pond 2, and Pond 4 (Table 1, Fig. 2).

Of the adult females that we sampled, 17% ($n = 601$) were gravid (estimated as $1 - \phi$ from the ZINB model fit to all data). There was a significant interaction of site and date on the

Table 1. A summary of data, model inputs, and simulations.

| Data | Pond 1 | Pond 2 | Pond 3 | Pond 4 | Town |
|--------------------------------------|------------|------------|---------------|--------|-------------|
| Number _t | 219 | 134 | 1470 | 68 | 1654 |
| Proportion(gravid) | 0.19 | 0.22 | 0.43 | 0.01 | 0.07 |
| #eggs gravid | 49 | 42 | 61 | 51† | 53 |
| Number _{t+1} , $p(s) = 0.1$ | 102 | 62 | 1928 | 2 | 307 |
| Number _{t+1} , $p(s) = 0.5$ | 510 | 310 | 9640 | 9 | 1534 |
| Number _{t+1} , $p(s) = 0.9$ | 918 | 557 | 17,351 | 16 | 2761 |

Notes: The bottom three rows are simulated numbers of adult female mosquitoes in the next generation (Number_{t+1}) at different levels of immature survival probability ($p(s)$). Here, we were assuming a 50:50 sex ratio (see Appendix S1: Table S3 for consideration of different sex ratios). Bolded values indicate positive population replacement rates.

Number_t is the total number of female mosquitoes collected at each site from 12, 18, and 25 June 2012. Proportion(gravid) and #eggs|gravid were estimated from the zero-inflated negative binomial models.

† No data were available for Pond 4, so we used the average egg number from the other sites.

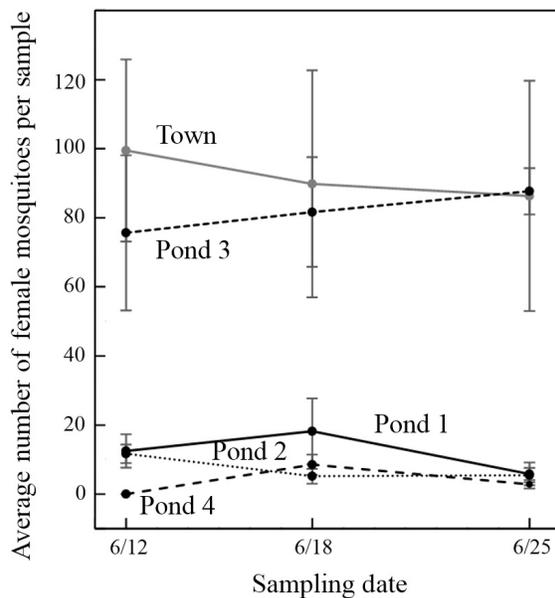


Fig. 2. The numbers of adult female mosquitoes collected using sweep nets were highest at the Town and Pond 3 sites but consistent among sampling dates. Points represent the average number of mosquitoes from the six sweep samples, and error bars are the standard errors of each mean.

proportion gravid ($\chi^2 = 28.1$, $P = 0.0002$), and significant main effects of site ($\chi^2 = 186.0$, $P < 0.0001$) and date ($\chi^2 = 95.3$, $P < 0.0001$; Fig. 3). Only one gravid mosquito was found at Pond 4 on 18 June (overall proportion = 0.01). As this prohibited fitting the ZINB model with site as a predictor variable, we removed Pond 4 before fitting the ZINB model by site. We also fitted the ZINB model to data from 18 and 25 June only, as the low numbers of gravid mosquitoes found on 12 June were probably because they had only recently emerged as adults. Based on the ZINB model, the proportion gravid was significantly higher at Pond 3 (0.43, 95% CI = 0.30–0.58) compared to Pond 1 (0.19, 95% CI = 0.10–0.33), Pond 2 (0.22, 95% CI = 0.13–0.34), and Town (0.07, 95% CI = 0.04–0.12; Table 1).

The average number of eggs per gravid female was 60 (estimated as λ from the ZINB model fit to all data) but was significantly higher at Pond 3 compared with all other sites ($n = 61$, compared to $n = 49$ at Pond 1, $n = 42$ at Pond 2, and $n = 53$ at Town; Fig. 4, Table 1). Residual variation in

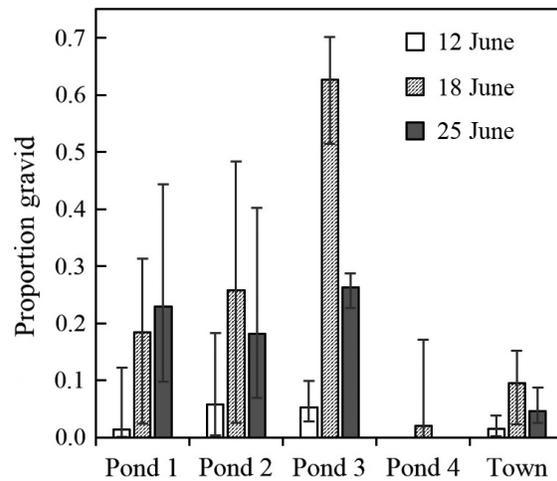


Fig. 3. Each bar represents the proportion of females that were gravid at each site and date (open bars = 12 June; hashed bars = 18 June; filled bars = 25 June) estimated by a full binomial regression model fit to all data. The error bars are the 95% confidence intervals for the parameter estimates and show that the proportion gravid varied among sites but was also dependent on date.

the number of eggs per gravid female was explained by body size ($R^2 = 0.20$, $P < 0.0001$); however, the site where mosquitoes had the greatest number of eggs per gravid female (Pond 3) did not have the largest mosquitoes. Mosquitoes were significantly larger (mean \pm SE) at Pond 2 (0.90 ± 0.05 mg) compared to all other sites (ANOVA: $F_{3,478} = 10.7$, $P < 0.0001$, proc mixed, Tukey adjustment for multiple mean comparisons, SAS v. 9.4). Mosquitoes at Pond 3 were the next largest (0.73 ± 0.01 mg), followed by mosquitoes at Pond 1 (0.63 ± 0.03 mg) and Town (0.65 ± 0.02 mg).

At all sites except for Pond 4, population growth rates could theoretically reach or exceed the replacement rate of $R = 1$ (Table 1, Fig. 5) at survival rates from egg to adult that were within empirical measurements from previous studies (0.01–0.40; Appendix S1: Table S2; Fig. 5). These results were robust to varying the sex ratios of females to males (Appendix S1: Table S3). Only the population from Pond 3 was estimated to be capable of growth ($R > 1$; Table 1, Fig. 5) within the lower range of survival probabilities, values that were most often measured in the field (< 0.11 ; Appendix S1: Table S2). At Ponds 1 and 2 (shown

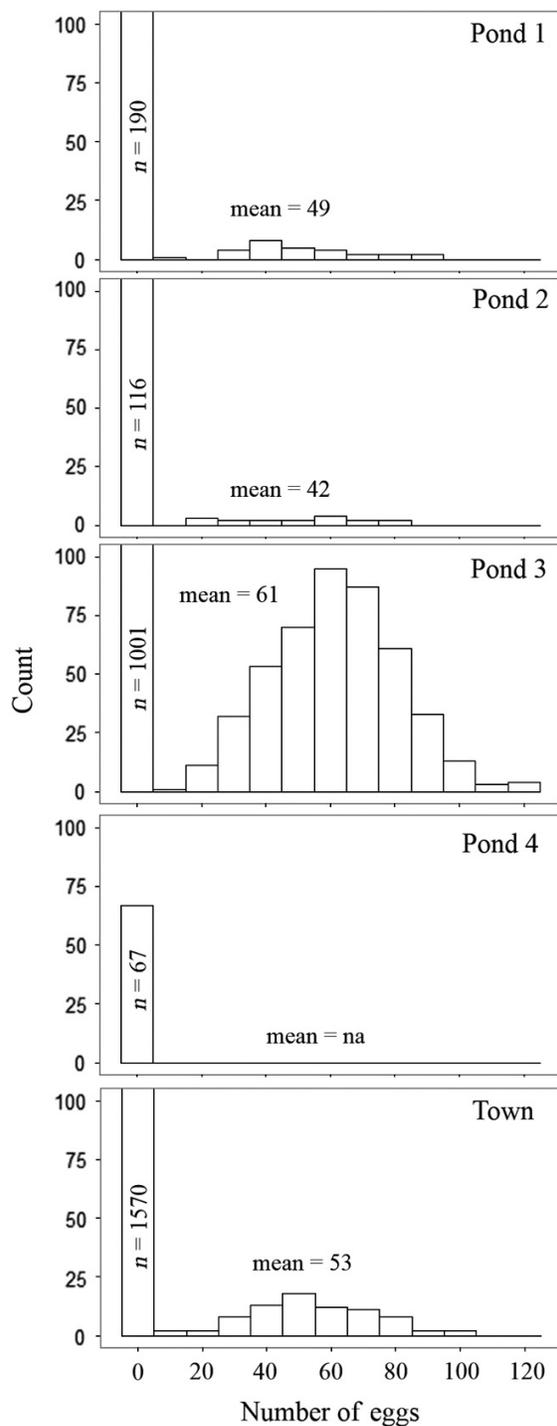


Fig. 4. Frequency distributions of the number of eggs in 3545 female mosquitoes. If a female was gravid (17%, $n = 601$), she had on average 60 eggs, but this varied among sites.

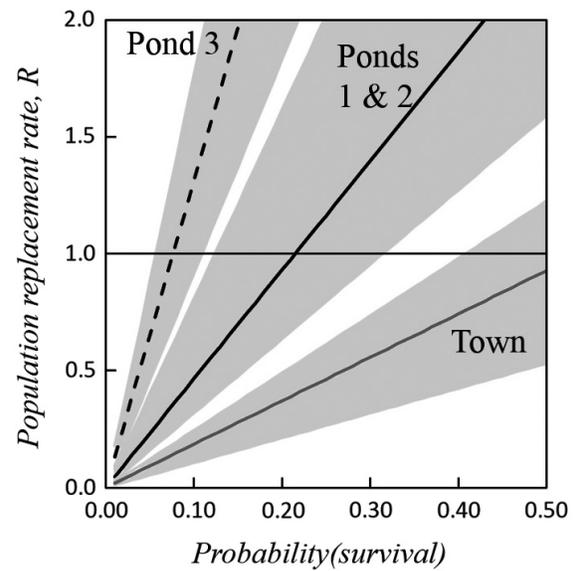


Fig. 5. Population replacement rates (R from eq. 1, y -axis) increased with immature survival probability (x -axis), but the rate of increase varied among sites where mosquitoes had significantly different probabilities of being gravid. Shaded areas represent 95% confidence intervals of $p(\text{gravid})$ estimated from the zero-inflated negative binomial model.

together in Fig. 5 due to similarity), 22% (95% CI 14–39%) of eggs would need to survive to the adult stage to reach replacement reproduction ($R = 1$). At Town, replacement seemed less probable because it required survival of 54% (95% CI 32–95%; Fig. 5), which is higher than any of our field estimates (Appendix S1: Table S2). Female mosquitoes at Pond 4, due to the very low probability of being gravid, would not reach replacement rate even if all of their eggs survived (for simplicity, not shown in Fig. 5).

DISCUSSION

We found conspicuous variation in the relative abundances of mosquitoes and the proportion that were gravid among our five tundra sites. All the mosquitoes we collected were female. Males can be shorter-lived than females (Maciel-de-Freitas et al. 2007) and often emerge earlier than females (e.g., Culler et al. 2015). Thus, it is likely that few, if any, males survived long enough to be captured during our sampling. We also found

consistent differences in the numbers captured among our sites (Fig. 2). Environmental conditions can influence insect captures from sweep-netting (Chaves et al. 2015), and we guess that the low numbers collected at Pond 4 were partly a result of colder, windier environmental conditions near the Greenland Ice Sheet (Culler et al. 2015, Fig. 1). However, our other sites had similar abiotic environments and we sampled them all within a few hours on each sampling date while the weather was stable. We doubt that the generally high variation in mosquito captures among sites was an artifact of sampling conditions.

We found the highest relative abundances at Pond 3 and Town. In the vicinity of Pond 3 and in Town, we recorded high densities of adult females on each sampling date (>7-fold higher than the three other study sites). Pond 3 lies within a low-lying valley (Fig. 1) where aquatic habitat is notably abundant, especially when compared to the Town location (L. E. Culler, *personal observation*). Thus, the adult mosquitoes that we captured near Pond 3 could have been produced locally, whereas the mosquitoes collected in Town were likely to have dispersed from some distance. The reason why mosquito abundances were so high at Town cannot be because mosquitoes were artificially attracted to light. Our site is above the Arctic circle and thus was receiving 24 h of daylight during the period of our sampling. However, there were always a few hundred potential vertebrate hosts (humans) in the immediate area of Town, which is an order of magnitude more host biomass than we have ever seen in the same area around Pond 3 (19 km away; Fig. 1). The high numbers of mosquitoes collected in Town may have been from host-seeking dispersal, which in tundra mosquitoes can occur over kilometers, often aided by wind (Blanton et al. 1950, Travis et al. 1950).

We were surprised then that the proportion gravid in Town (0.07) was so much lower than the proportion gravid at Pond 3 (0.43). At each of these sites, the average number of eggs per gravid female (61 at Pond 3 and 53 at Town) was significantly higher than the number of eggs matured via autogenous reproduction in this species (1–16 eggs; Corbet 1964, 1967). Thus, we infer that the gravid mosquitoes had likely matured their eggs after successfully obtaining a blood meal (further discussed below). If so, this

suggests that although humans may give off a signal of being a host, they are better defended from mosquito feeding vs. Greenlandic wildlife (Corbet and Downe 1966, Edman et al. 1974). Although we did not quantify the number of vertebrate hosts at our sites, we more frequently observed caribou, muskox, hare, and waterfowl, all potential hosts for *Aedes nigripes* (Corbet and Downe 1966), at Pond 3 compared to Town and other locations where the proportions gravid were considerably lower (Table 1).

The number of eggs per gravid female was a function of site and size. The fecundity of mosquitoes that obtain a blood meal is related to their adult mass prior to the blood meal (e.g., Livdahl 1982). Adult body size is also an indication of food availability and larval densities in aquatic habitats (e.g., Leonard and Juliano 1995, Strand et al. 1999). There was strong heterogeneity in adult body size among our study sites: Adult females near Pond 2 and Pond 3 had about 41% and 14% (respectively) greater mass than at Pond 1 or Town. Based on the variation in body size, it was expected that there would be corresponding variation in the number of eggs per gravid female. This prediction was partly satisfied in that gravid females from Pond 3 produced about 20% more eggs than those from Pond 1 or Town. However, Pond 2, where mosquitoes were the largest, did not have the highest number of eggs per gravid female. This could be partly an artifact of the small sample at Pond 2 (only 29 gravid females at Pond 2 vs. 630, 115, and 42 at Pond 3, Town, and Pond 1, respectively), but also suggests that factors in addition to body size at emergence might influence the fecundity of Arctic mosquitoes. The host species from which blood was obtained could be one additional factor (Takken and Verhulst 2013). Another possibility has been described as carry-over effects (e.g., Westby and Juliano 2017) in which the quality of larval habitats continues to influence fitness in the adult life stage. In our case, this might predict that the nutritional quality of food is different and higher in Pond 3. A further implication of the spatial heterogeneity in adult body size is that dispersal of adult mosquitoes must not be so great that it swamps the effects on body size from local larval habitats.

Although autogeny has evolved in several different clades of biting insects in the north (Downes 1958, Davies 1961), including *A. nigripes* on

Ellesmere Island to the west of Greenland and at a higher latitude (Corbet 1964, 1967), it is apparently rare or absent in our study population. We did not find evidence for a bimodal distribution in the number of eggs per female (i.e., Fig. 4 would have shown a lower mode centered on 1–16 eggs; Corbet 1964, 1967). Autogeny is a presumed adaptation in locations and years where blood meals are very scarce (Corbet 1967). We estimate that our population can persist or grow without autogeny if more than about 30% of adult females succeed in obtaining a blood meal. Data such as in Fig. 4 and experimental tests of the capacity for autogenous reproduction in diverse Arctic locations could permit tests of life-history theory for the evolution of autogeny in blood-feeding insects.

Understanding the abundance of *A. nigripes* across the landscape requires more research about the spatial patterns and drivers of immature survival and the spatial heterogeneity of vertebrate hosts and reproduction. The modeling results suggest that our study system is a mosaic of areas that are local sources for mosquitoes ($R > 1$; e.g., Pond 3) and others that are sinks ($R \ll 1$; e.g., Town, Pond 4). The variation in population change (R) was a function of similarly strong effects from variable survival and growth of immatures in aquatic habitats and variation in fecundity. For example, estimated R at an average immature survival of 0.11 ranged by about 10-fold from well above replacement rate (≈ 1.30) to way below replacement rate (≈ 0.25) due to differences in fecundity at Pond 3 vs. Town. Similarly, estimated R at an average probability of being gravid (0.17) also ranged by about 10-fold (≈ 1.35 vs. 0.25) due to differences between a pond with median immature survival (0.04) and one with relatively high survival (0.30; Appendix S1: Table S2). One hypothesis is that the quality of larval and adult habitats will tend to be negatively correlated across the landscape; areas with easy access to vertebrate hosts will tend to be areas with the highest density of hatching eggs, and therefore, competition for food among larval mosquitoes will be highest (such as at Pond 3). For *A. nigripes*, predation and temperature are known to affect immature survival (Culler et al. 2015), but very little is known about the influence of resource quantity and quality on growth and survival. At our sites with intermediate values of abundance and fecundity (Ponds 1 and 2), lower

larval densities and higher food availability may promote higher survival such that replacement reproduction is still possible even with low adult fecundity. At Pond 4, which is closest to the ice sheet (Fig. 1), colder water temperatures may lower immature survival rates (Culler et al. 2015) and windier, colder conditions during the adult stage may restrict adult feeding behavior (Witter 2010, Witter et al. 2012), resulting in a local sink population.

Aquatic habitat and vertebrate host availability, both of which are responding to rapid Arctic environmental change (e.g., Smol and Douglas 2007, Post and Forchhammer 2008), will significantly impact Arctic mosquito populations, especially in the absence of autogeny. Temporary ponds that are habitat for immature Arctic mosquitoes are changing in size due to warming, permafrost melt, and changes in precipitation (Smol and Douglas 2007, Melillo et al. 2014, Andresen and Lougheed 2015), which will determine the relative importance of adult reproduction vs. immature survival in determining abundance. Warmer conditions will also lead to an earlier emergence of mosquitoes (Culler et al. 2015), which may alter their synchrony with potential vertebrate hosts that may or may not respond similarly to changing conditions. For example, the timing of caribou calving (which presumably brings about an increase in blood meal availability) does not respond to warming in the same way as ectotherms (Post and Forchhammer 2008), such as mosquitoes. Thus, the average fitness of mosquitoes and the potential for population change is a function of climate effects on aquatic and terrestrial mosquito habitats.

In the Arctic, and throughout the world, mosquito response to environmental change is key for understanding their future impacts on humans and ecosystems. For the tundra ecosystem in our study, changes in mosquito abundance could significantly impact taxa that rely on immature and adult mosquitoes as a food source (Culler et al. 2015), plants that are insect pollinated (Urbanowicz et al. 2017), and wildlife that are interminably harassed by mosquitoes (Helle and Tarvainen 1984, Witter et al. 2012). Understanding and anticipating changes in Arctic ecosystems will be enhanced by characterizing the mechanisms that govern phenology and abundance of this globally notable clade.

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