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Population Regulation and Density-Dependent Demography in the Trinidadian Guppy

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ABSTRACT: Classic theory for density-dependent selection for delayed maturation requires that a population be regulated through some combination of adult fecundity and/or juvenile survival. We tested whether those demographic conditions were met in four experimental populations of Trinidadian guppies in which delayed maturation of males evolved when the densities of those populations became high. We used monthly mark-recapture data to examine population dynamics and demography in these populations. Three of the four populations displayed clear evidence of regulation. In all four populations, monthly adult survival rates were independent of biomass density or actually increased with increased biomass density. Juvenile recruitment, which is a combination of adult fecundity and juvenile survival, decreased as biomass density increased in all four populations. Demography showed marked seasonality, with greater survival and higher recruitment in the dry season than the wet season. Population regulation via juvenile recruitment supports the hypothesis that density-dependent selection was responsible for the evolution of delayed maturity in males. This body of work represents one of the few complete tests of density-dependent selection theory.

Keywords: demography, density-dependent evolution, guppies, population dynamics, population regulation.

Introduction

The density-dependent evolution of life histories has a long history in theory but a sparser history of empirical tests in nature (Bassar et al. 2010; Travis et al. 2013). Part of the reason for this disparity is the difficulty of testing the theory. The theory's predictions rest on three conditions. First, the focal population must be strongly regulated (Macarthur 1962). Second, the demography of density regulation must be quantified; the specific predictions offered by theory depend on the stage of the life cycle in which the population is most strongly regulated (Charlesworth 1994; Engen and Saether 2016, 2017). Third, the stage in the life cycle in which regulation is strongest must be shown to contribute heavily to the fitness differences among phenotypes (Engen and Saether 2016).

The second condition is especially important. If the deleterious effect of density is equal across all stages of the life cycle, selection will not favor a life history different from that of an unregulated population (Michod 1979). More generally, the precise theoretical prediction depends on where density acts most strongly in the life cycle. Consider what is necessary, in theory, for density-dependent selection to favor delayed maturity, assuming that delayed maturity can increase reproductive capacity. Selection will favor a delay in a regulated population if increased density increases juvenile mortality or decreases adult fecundity; selection will not favor a delay if increased density only decreases adult survival (Charlesworth 1994). A heuristic explanation for this distinction is that in the former cases, a delay in maturation will increase the per capita fecundity and the production of juveniles, thereby countering the deleterious effects of density. However, in the latter case, a delay in maturation will not increase the density of adults, thereby offering no counter to the deleterious effect of density.

The difficulty of fulfilling the second condition is the factor most responsible for the gap between theory and data. There are hundreds of studies of regulation in natural populations and density-dependent demography (Brook and Bradshaw 2006; Ziebarth et al. 2010; Knape and de Valpine 2012; Thibaut and Connolly 2020), but few of these include a focus on density-dependent evolution (Bassar et al.

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2010). There are hundreds of studies that examine phenotypic performance—and sometimes fitness—as a function of density (Herrando-Perez et al. 2012*a*, 2012*b*), but only a few, like those of Saether et al. (2016) and Kentie et al. (2020), are connected directly to studies of numerical dynamics and demography (Bassar et al. 2010).

As a result, while the concept of density-dependent life history evolution has captured the imagination of geneticists and ecologists for almost 60 years (Macarthur and Wilson 1967; Pianka 1970; Roughgarden 1971; Michod 1979; Boyce 1984; Charlesworth 1994), we have only a small number of convincing demonstrations of its importance in nature. Density-dependent selection that varies temporally and spatially governs the dynamics of egg size and other life history traits in side-blotched lizards, *Uta stansburiana* (Sinervo et al. 2000; Svensson and Sinervo 2000). Saether et al. (2016) showed that selection favored different clutch sizes in a population of great tits at different densities, and Kentie et al. (2020) demonstrated that selection favored different asymptotic body masses in Soay sheep at different densities. The most comprehensive evidence for density-dependent evolution is the adaptive plasticity of the elongation response in *Impatiens capensis* (Dudley and Schmitt 1995, 1996; Donohue et al. 2000*a*, 2000*b*).

Trinidadian guppies, *Poecilia reticulata*, offer an excellent opportunity to address this imbalance (Travis et al. 2014; Reznick and Travis 2019). In higher-order streams draining the slopes of the Northern Range Mountains of Trinidad, guppies co-occur with a diverse community of predators. Natural barriers limit the upstream dispersal of those predators so that in the lower-order streams throughout the mountains, guppies live at higher densities largely without predators. There are genetically based differences between the life histories of high-predation and low-predation populations: guppies in low-predation streams mature later and larger, exhibit more color (males), and produce fewer but larger offspring (females; Endler 1978; Reznick 1982; Reznick and Endler 1982; Reznick et al. 2001; Reznick and Travis 2019).

Population genetic studies indicate that guppies have moved upstream from high-predation habitats to low-predation habitats independently in different drainages (Alexander et al. 2006; Willing et al. 2010), suggesting that these life history differences have evolved repeatedly. Two independent introductions of high-predation guppies into low-predation habitats, which simulated this natural process of upstream colonization, have shown that the descendants of the introduced fish rapidly evolved life histories characteristic of natural low-predation populations (Reznick and Bryga 1987; Reznick et al. 1990; Reznick et al. 1997).

New experimental evidence suggests that the rapid evolution of delayed male maturation is driven by density-dependent selection. In 2008 and 2009, we created four experimental populations of guppies by extending their range in the Guanapo River system above barrier waterfalls that previously excluded guppies (Reznick et al. 2020). We placed guppies collected from a downstream, high-predation location into each of four separate upstream tributaries at very low initial densities. Over the next several years, we watched the numbers of guppies in these experimental populations increase. Each year, we collected juveniles from each experimental population and from the downstream, high-predation site of origin for laboratory common-garden experiments with their grandoffspring (Reznick et al. 2019*a*). Initially, we found significant additive genetic variation within each population for age at maturity. In subsequent years, we found that males from the experimental populations displayed increased age at maturity in the common garden, contrasted with males from the downstream site of origin. However, those increases appeared only after the biomass densities in the experimental populations had increased to high levels in the third year after the establishment of the populations.

Quantitative genetic evidence from the field is consistent with the common-garden evidence (Potter et al. 2021). We used 46 microsatellite loci to build a long-term pedigree for all of the individuals in one of the four experimental populations (Reznick et al. 2020). First, the founding population had significant variance in the breeding values for male size at maturity, which is tightly correlated with the age at maturity (we cannot measure age at maturity in the field). Second, the breeding values for size at maturity increased with time but only after the population density in that stream reached a very high level, which occurred in the third year after establishment.

Further evidence for evolutionary change in these experimental populations was found in whole-genome studies of individuals collected in 2013, 4–5 years after the establishment of the experimental populations (van der Zee et al. 2022). There were convergent changes in allele frequencies in all four experimental populations, compared with individuals from the downstream site of origin, in an area of chromosome 15 and strong statistical evidence of selection in that genomic region in three of the four populations.

These results establish that evolution occurred in these four experimental populations and suggest that density-dependent selection was the driving force. To test that hypothesis, we must show that regulation in these four experimental populations occurred through the effect of increased density in reducing adult fecundity or increasing juvenile mortality. This requires a long-term study of demography and population dynamics. Short-term observational studies in natural environments do not provide sufficient power to distinguish density dependence in population dynamics from the effects of stochastic variation (Brook and Bradshaw 2006; Knape 2008; Ziebarth et al. 2010). Short-term experiments examining the response to perturbations of population density may create changes in density that are larger (or smaller) than the magnitude of typical fluctuations in density in nature and thus provoke misleading conclusions about the strength of regulation and its location in the life cycle (Fowler et al. 2006).

Here, we show that density regulation in these four experimental populations was attained via juvenile recruitment rather than adult survival, which is the requirement for density-dependent selection to favor delayed maturity. We thus unite our evolutionary studies of life history evolution with an ecological study of numerical dynamics and demography, bringing empirical data together with classic theory.

Material and Methods

Experimental Design and Execution

We introduced guppies into two pairs of streams, one pair in 2008 and the other pair in 2009. We thinned the canopy of one stream in each pair to test the hypothesis that guppy populations under natural (intact) canopies are resource limited. Under this hypothesis, thinned canopies should promote higher population densities through higher light levels and increased primary productivity (Kohler et al. 2012; Collins et al. 2016). We introduced 38 males and 38 females each into the Lower LaLaja River (LLi; intact canopy) and the Upper LaLaja River (ULt; thinned canopy) in 2008. We introduced 52 males and 52 females each into the Caigual River (CAi; intact canopy) and Taylor River (TAt; thinned canopy) in March 2009.

We collected the fish for each introduction into each pair in January 2008 (LLi and ULt) or 2009 (CAi and TAt). We collected juveniles and reared them to maturity in single-sex groups in the laboratory. As the fish matured, we combined them into groups of five males and five females 2 weeks before the introduction to allow mating. We marked each fish as an individual with subcutaneous dots of colored elastomer (Northwest Marine Technologies). When we introduced the fish, we placed the females and males from the same mating group into different streams. For example, in 2008, we placed females from one particular mating group into LLi and males from that same mating group into ULt. This means that we introduced the genome of each male into both streams in a pair, in one case as the male himself and in the other as either fertilized embryos or stored sperm in the females from his mating group.

We censused all populations monthly, beginning 1 month after the introduction and continuing through 103 months afterward. We collected the fish in a spatially explicit fashion, noting their locations along the length and width of the stream. We placed males and females collected at each location in separate labeled containers filled with medicated stream water for transport back to the laboratory. We kept each group of fish separate from other fish throughout processing, returning them after processing to their location of capture.

In the laboratory, we weighed and photographed all captured fish. We identified captured fish marked in previous censuses. We considered newly captured, unmarked fish that were at least 14 mm long to be new recruits to the adult population and gave them their own individual marks. An individual guppy requires about 6 weeks to grow from its length at birth (~7 mm) to the minimum adult size of 14 mm. Further details of these methods are presented elsewhere (Reznick et al. 2019*a*, 2020).

Statistical Analyses

We used total biomass density as our measure of population density for all analyses. Male and female guppies differ in body size; somatic growth in guppy females is indeterminate. These facts mean that the pressure on a habitat's resources will depend not only on the number of guppies but also on the sex ratio and the distribution of body sizes in each sex. Prior work has shown that the demographic rates of guppy populations depend on body size distributions (Bassar et al. 2013, 2016), that competitive interactions among individuals depend on their relative body sizes (Potter et al. 2019), and that population projections incorporating size-based interactions outperform projections that do not (Griffiths et al. 2020).

We used the program MARK (White and Burnham 1999) to estimate biomass densities and monthly adult survival, all corrected for the estimated probability of capture by dividing initial estimates by the capture probability. We estimated sex-specific survival and probability of capture in each census period using the Cormack-Jolly-Seber module of MARK, as implemented in R (Laake 2013; R Development Core Team 2020). We ran fully time-dependent models of survival and probability of capture for each stream and crossed period with sex, using the default parameter settings for each model. We estimated the corrected numerical density of individuals of each sex in each month by dividing the estimated number of individuals of each sex, divided by the probability of capture, by the total benthic area of each stream, measured as described elsewhere (Reznick et al. 2020). Our high monthly capture rates (figs. S1, S2) minimized any systematic bias in these estimates. We estimated the biomass density of each sex in any given month by multiplying the corrected numerical density of each sex in that month by the average mass of the individuals of that sex captured in that month. We calculated total biomass density by adding the biomass densities of males and females. The sampling variance of total biomass density is a function of the sampling variances of numerical density for each sex and those of mean body mass for each sex; the supplemental PDF describes how we calculated this variance.

We used the cumulative variance of biomass density to divide each time series into an early period of steady initial growth and a late period of bounded fluctuations. When the cumulative variance approaches an asymptote, a population has entered a period of bounded fluctuations (Denboer 1991; Murdoch 1994). Density-dependent responses produce bounded fluctuations, but bounded fluctuations themselves need not indicate density dependence (Denboer 1991). A drop in the cumulative variance from its peak value occurs when the initial values of density in a census are outside the range of the long-term bounded fluctuations (Murdoch and Walde 1989).

We defined the early period for each population as the time from introduction until the biomass density in that population attained its peak value of cumulative variance (Murdoch and Walde 1989; Murdoch 1994). We defined the late period for each population as the period from the month after attainment of peak cumulative variance to month 103. Dividing the data in this manner carries the risk of overestimating the importance of density dependence in the complete trajectory of population dynamics. However, our goal was not to estimate the relative strength of density dependence in the complete trajectory but to examine the demography of these populations in the period in which they displayed bounded fluctuations, which is also the period when delayed male maturity appeared in the common gardens.

Assessments of density dependence require separating sampling—or observational—variance from the genuine temporal variance in densities, usually called the "process" variance. Sampling variance, if large compared with the process variance, can increase the probability of a type I error in detecting density dependence (Dennis et al. 2006; Freckleton et al. 2006; Knape 2008; Tenan et al. 2019).

We used state-space models, which separate these variances, to test for density-dependent dynamics. Specifically, we used state-space models of the first differences in log total biomass density (Holyoak and Baillie 1996; Ziebarth et al. 2010). For each population's time series, we compared models of a random walk, which is the simplest density-independent process, with models of density dependence. Using the first differences means that we were testing whether the change in log total biomass density between one month and the next depended on the change between that month and the preceding month. There will be no such dependence in a random walk, in contrast to a density-dependent process (Dennis et al. 2006). We provide a fuller description of these models in the supplemental PDF.

We fit our state-space models in R (R Development Core Team 2020), using the package dlm (Petris 2010; Auger-Methe et al. 2021). The package estimates three parameters from a time series of first differences: the sampling—or observational—variance, the process variance, and the autoregression coefficient. The autoregression coefficient relates differences between sequential pairs of months to each other. We reduced the number of parameters estimated by specifying the observational variance from the sampling variances of numerical density and mean body mass (supplemental PDF).

We fit six models to the data for each stream, three models of a random walk (density-independent dynamics), and three models of a stochastic Gompertz equation (density-dependent dynamics; Dennis et al. 2006). For each type of model, we set three different observational variances: twice the value of the actual observational variance of log biomass data, as calculated from the data, appropriate for analyzing first differences (supplemental PDF); one-quarter of that value; and four times that value. Using a range of values allowed us to assess the robustness of our estimates of the value of the autoregression coefficient, which we label as c. For the models of random walks, we constrained the value of c to be 1.00; $c = 1$ indicates that sequential differences in log density are unchanged except by further random perturbation. Density dependence creates a stationary distribution of first differences with a value of c between -1 and $+1$ (supplemental PDF); this range of values indicates that sequential differences grow smaller with each time step, absent further random perturbation.

We fit models using maximum likelihood and compared the six models via the Akaike information criterion (AIC), as described in Auger-Methe et al. (2021). We varied the initial values assigned to the estimated parameters (process variance and, for density-dependent models, c) to ensure that the models alighted on the peak likelihood. From each model, in addition to the parameter estimates, we used the Kalman filter to estimate the true values of total biomass density for each month.

We checked the fit of the model with lowest value of AIC in three ways. First, we examined plots of estimated versus observed values. Second, we examined quantile plots of a normal distribution of residuals. Third, we examined the one-step-ahead residuals from the Kalman-filtered estimates for any autocorrelation structure. In all cases, estimated and observed values were well correlated except that some observed values of peak density and troughs in density were higher or lower, respectively, than the estimated values. This produced a more leptokurtic distribution of residuals than a desirable normal distribution. In no case was there any autocorrelation structure among the one-step-ahead residuals.

We analyzed monthly male survival, monthly female survival, and monthly per capita female recruitment rates (number of new recruits divided by the number of sexually mature females) as functions of total biomass density in the preceding month to look for where the deleterious effects of increased biomass density would be strongest. We also analyzed recruitment rate as a function of biomass density 2 months prior. Guppies grow from their length at birth (~7 mm) to the minimum adult size (~14 mm) in about 6 weeks; if the effects of biomass density affected survival of neonates and small juveniles, those effects might be more visible with a 2-month lag.

These analyses were complicated by the fact that the values of each variable and biomass density were estimates with associated sampling variances. In such a case, the point estimates of each variable and biomass density could be at the extremes of the sampling distribution for these quantities, making suspect the results of a simple regression analysis of the point estimates.

To assess this possibility, we used R (R Development Core Team 2020) to draw 1,000 random samples of each variable and of biomass density from a normal distribution specified by the mean and sampling variance of each quantity. For male and female survival, we used logit-transformed values to allow us to use a normal distribution. For each random sample, we regressed the randomly drawn demographic value on the randomly drawn value of biomass density. We used model 1 regressions in these simulations because model 2 regressions require sampling variances of the independent and dependent variables to be equal (Legendre and Legendre 1998), which they were not in our data. We compared the slope of the regressions with the actual point estimates to the 95% range of the slopes of the random samples.

Given that this analysis revealed that the point estimates were typical representatives of the sampling distribution, we continued analyses of demographic rates with the point estimates. We used ANCOVAs to test whether the demographic variables were functions of both season and biomass density. We assigned one of four seasons to each month's sample: dry season (February–May), transition from dry to wet season (June and July), wet season (August–November), and transition from wet to dry season (December and January). The precise monthly durations of wet and dry seasons varies year to year, but this demarcation was a reasonable first approximation.

To make these tests, we first fit a full model to each demographic variable (using logit-transformed values for survival) using the predictors season, total biomass density in the previous month, and their interaction. In no case was the interaction statistically significant, and in no case was the *F* statistic for that interaction greater than 1.0, so we report the results from models using only the two main effects. We made statistical tests on the type III sums of squares, assessing the significance of each main effect in the presence of the other, using the software package SYSTAT 12.0. In the "Results," we present least squares means for these models. For survival, we present least squares means on the original scale, after back transformation, calculating the back-transformed standard errors as described in the supplemental PDF.

Results

Capture Probabilities

Most of the monthly capture probabilities were above 0.80, with many approaching 1.0 (figs. S1, S2). The high average monthly capture probabilities also had very small standard errors, which produced small sampling variances for biomass density and the demographic rates (figs. 1, S1–S5).

Initial Population Growth

The differences among our four streams in area produced different densities of individual guppies and biomass. The 76 fish initially introduced into the first pair, LLi and ULt, corresponded to about 0.18 and 0.14 guppies m^{-2}, respectively, or a biomass density of about 0.027 and 0.016 g m^{-2}, respectively. The 104 fish introduced into the second pair, CAi and TAt, corresponded to about 0.65 and 0.74 guppies m^{-2}, respectively, or a biomass density of about 0.105 and 0.136 g m^{-2}.

All four populations grew rapidly (fig. 1). The estimated peak biomass densities ranged from about 0.51 g m^{-2} (about 2.9 guppies m^{-2}) in CAi to 1.44 g m^{-2} (about 8.5 guppies m^{-2}) at TAt. The geometric mean monthly growth rates of the two populations under thinned canopies, ULt and TAt, were 1.16 and 1.13, respectively. These rates were higher than the monthly rates in their corresponding populations under intact canopies, LLi and CAi, each of which displayed a growth rate of 1.08. The pair initiated at the lower densities, LLi and ULt, reached the point of maximum cumulative variance in 32 and 29 months, respectively (fig. 2). The second pair, CAi and TAt, which were initiated at the higher densities, reached the same point in 21 and 15 months, respectively.

The Emergence of Population Regulation

In three of four populations (LLi, ULt, and CAi), the cumulative variance in population density decreased steadily

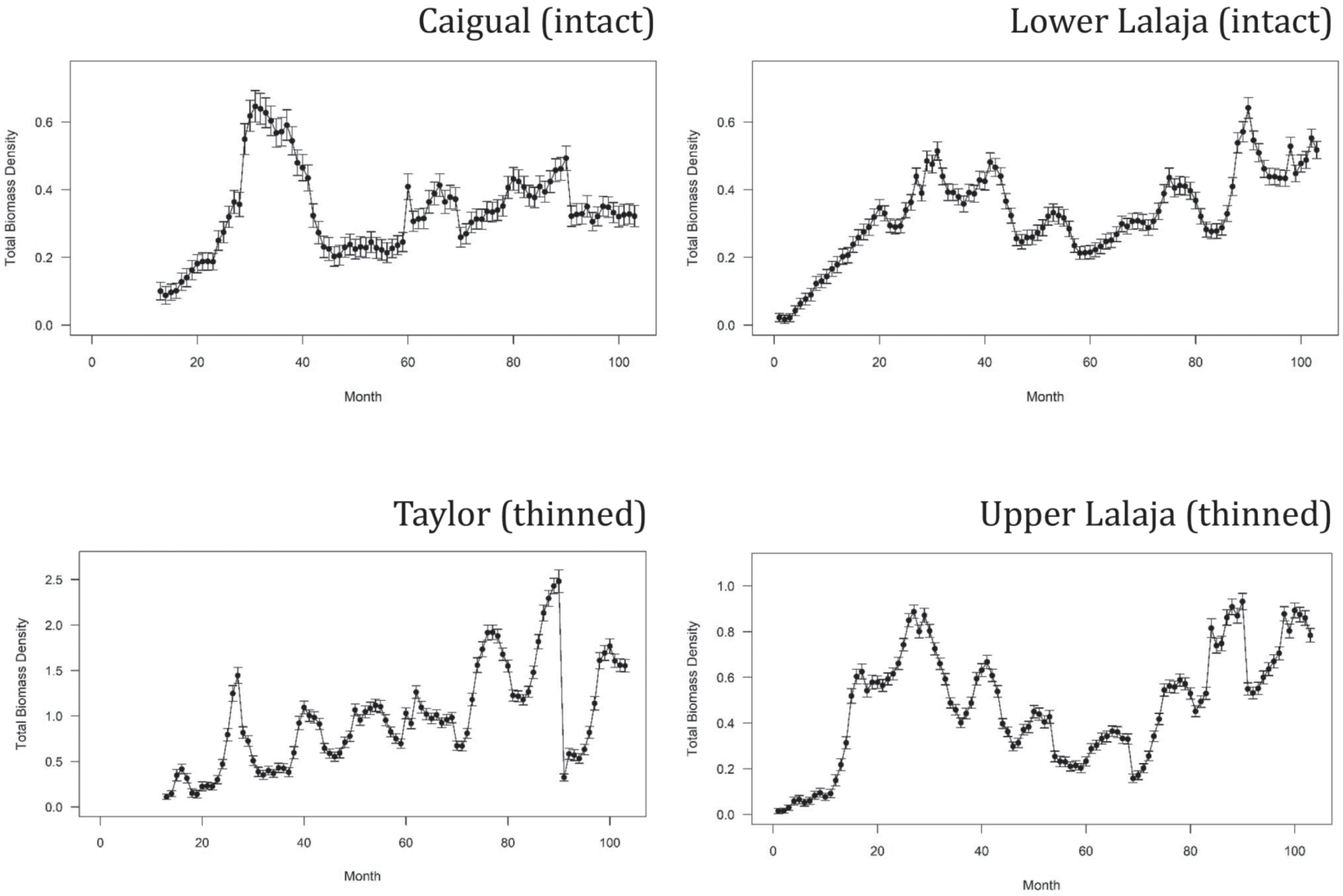


Figure 1: Total biomass density (g m^{-2}) in each month in each stream. Error bars represent 1 SE, calculated as described in the supplemental PDF. “Intact” and “thinned” refer to canopy conditions.

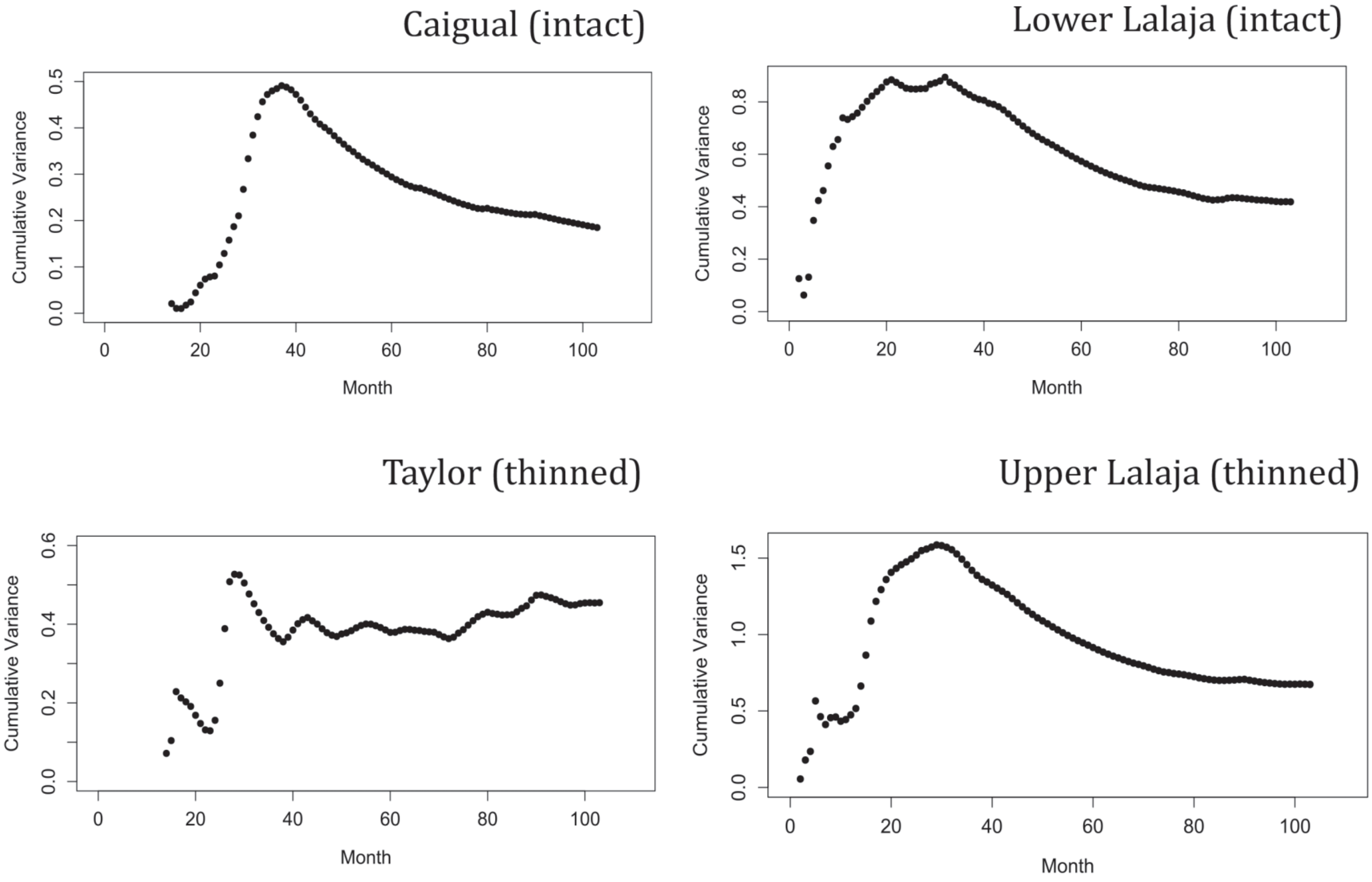


Figure 2: Cumulative variance of total biomass density across months. “Intact” and “thinned” refer to canopy conditions.

after the peak value (fig. 2). This indicates that these populations had entered a region of bounded fluctuations, consistent with but not necessarily indicative of regulation. In TAt, the cumulative variance decreased for a short period but then increased steadily thereafter. This pattern, combined with its general long-term trend toward increasing density (fig. 1), suggests that TAt had not attained a long-term steady state consistent with regulation.

The two populations under thinned canopies (TAt and ULt) experienced a sharp decline around sampling month 86, caused by unusual flooding (fig. 1). The other populations also displayed a decrease in density at month 86 but not of the same magnitude. The decline in month 86 aside, three of the four populations (LLi, TAt, and ULt) displayed seasonal fluctuations in density. These were most visible in the two populations under the thinned canopy, TAt and ULt. In all three cases, peaks occurred in dry season months (approximately months 40, 53, 64, 75, 85, 100) and troughs occurred in wet season months (approximately months 35, 47, 58, 70, 80).

For all four streams, a state-space model of density dependence fit the data better than models of random walks (table 1). There were either only small differences in AIC values among the three density-dependent models (CAi and LLi) or no differences at all (TAt and ULt). The estimates of the true values of the changes in biomass density hewed closely to the observed values (fig. 3). This is not surprising because the sampling variances were small. This was especially true in TAt and ULt, which had the smallest levels of sampling variance in total biomass density (fig. 1). In all but about a dozen months, the observed values were within the 95% confidence limits of the estimated values. In nearly all of these exceptional cases—like the case of month 86, in which there was a severe flash flood—the outliers reflected extraordinarily large decreases in total biomass density. The state-space model

Table 1: Results of fitting state-space models to each stream's time series of first differences in log total biomass density, three density-independent models (DI), and three density-dependent models (DD)

Stream and model	Observational variance	Autoregression coefficient	Estimated process variance	AIC
Caigual (intact):				
DI 1	.009	≡1	.0345	−138.59
DI 2	.018[a]	≡1	≈0	−190.65
DI 3	.036	≡1	≈0	−183.60
DD 1	.009	−.432	.0098	**−198.62**
DD 2	.018[a]	−.568	.0035	−196.21
DD 3	.036	. 110	≈0	−185.15
Lower Lalaja (intact):				
DI 1	.009	≡1	.0004	−145.12
DI 2	.018[a]	≡1	.0002	−174.75
DI 3	.036	≡1	.0002	−167.44
DD 1	.009	−.258	.0114	**−196.09**
DD 2	.018[a]	−.133	.0040	−193.80
DD 3	.036	.070	≈0	−185.19
Taylor (thinned):				
DI 1	.004	≡1	.1443	−62.26
DI 2	.008[a]	≡1	.1287	−64.22
DI 3	.016	≡1	.0978	−68.44
DD 1	.004	.047	.0782	−108.36
DD 2	.008[a]	.050	.0742	−108.36
DD 3	.016	.058	.0661	**−108.37**
DI 1	.004	≡1	.0423	−137.29
Upper Lalaja (thinned):				
DI 2	.008[a]	≡1	.0264	−144.14
DI 3	.016	≡1	.0071	−157.69
DD 1	.004	.073	.0272	−176.12
DD 2	.008[a]	.092	.0231	−176.14
DD 3	.016	.182	.0147	**−176.26**

Note: Boldface indicates the lowest AIC value. Canopy treatments for each stream are in parentheses.

[a] Value of observational variance estimated from original data.

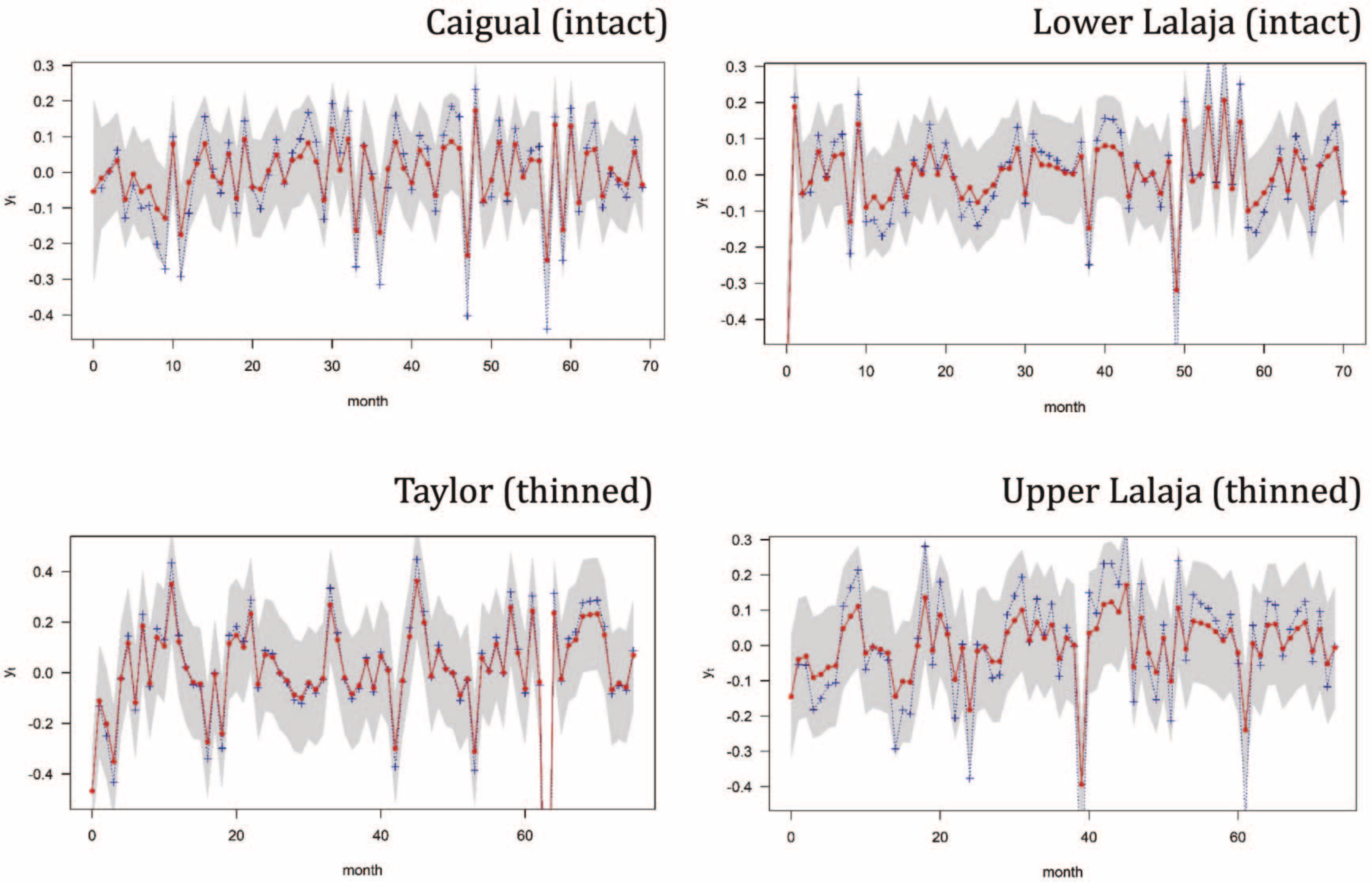


Figure 3: State-space models for first differences in log total biomass. On the axis "y_t," crosses represent the observed differences, and circles represent the estimated true values. Shaded areas represent the 95% confidence limits around the estimated values. "Intact" and "thinned" refer to canopy conditions.

offered robust estimates of the typical, monotonous fluctuations around a long-term average. The process model was not designed to take the occasional catastrophe into account, and it was at these events that the predicted and observed values differed most. The fit of the density-dependent models to the series of differences in TAt was the worst of the four cases. This is not surprising, given that TAt continued to show a long-term increase in density.

Demographic Patterns

Male Survival. Monthly survival rates of adult males varied, for the most part, between 0.60 and 0.80 in all four streams (fig. S3). Male survival rates were more variable in the initial months, particularly in the two populations under the thinned canopies, TAt and ULt. Two populations, CAi and ULt, exhibited scattered low values of male survival throughout the period of study.

There was no evidence that biomass density alone affected monthly male survival (fig. 4; table 2). The estimated slopes of the regressions of the random draws from the distributions of male survival and biomass density varied widely, and in no stream was the regression of the point estimates of survival on biomass density significant (table 2).

However, in three of the four populations (LLi, TAt, and ULt), there was a strong effect of season on male survival (fig. 5; table 3). Male survival rates were highest in the dry season and lowest in the wet season. Values in the wet season ranged approximately 12%–15% below those in the dry season. In the two populations under the thinned canopy (TAt and ULt), when we included the effect of season in the model, increased male survival was associated with increased biomass density.

Female Survival. Monthly female survival rates ranged between 0.80 and 0.99 for much of the period of study (figs. 5, S4) and were generally higher than those for adult males. As was the case for males, female survival rates were more variable in the initial months, especially at TAt. Aside from month 86, in which there was a sharp decline in biomass density, female survival held steady throughout the period in LLi and ULt, appeared to decrease late in the period in CAi, and increased throughout the period in TAt.

The overall relationship between biomass density and female survival varied among populations (fig. 6; table 2). In CAi, the estimated slopes of the regressions of the random draws from the distributions of female survival and biomass density varied widely, and the regression with the point estimate was not significant. The data from TAt displayed a similar pattern, although with less variation in slope among the regressions with the random draws than was seen in CAi. In LLi, the regression of the point estimate of female survival on biomass density was significant, revealing a positive relationship between biomass density and female survival and accounting for 14% of the variation in female survival. This was not an aberrant result; the slope of the point estimate was well within the range of slopes from the regressions on random draws. A similar result appeared in the overall analysis of female survival in ULt, although in this case the regression of the point estimates was much weaker, accounting for 6% of the overall variation in female survival.

Monthly female survival was less responsive to seasonal effects than monthly male survival (fig. 5; table 3). In general, like the pattern in males, female survival was lowest in the wet season, although the difference in average female survival between dry and wet season was only about 10%. When we included both season and biomass in a model for monthly female survival, survival increased significantly with density in LLi and ULt but not in CAi or TAt. Season was a statistically significant effect in every stream, although a weaker effect in TAt than in the others.

Recruitment Rate. The number of recruits per female varied in all four populations during the period of study but varied especially widely in the early months (fig. S5). The changes from one month to the next were often small but sometimes quite large, varying as much as two- to threefold.

There was a strong negative effect of biomass density on recruitment rates (fig. 7; table 2). The estimated slopes of the regressions of the random draws from the distributions of female survival and biomass density were uniformly negative and varied narrowly in all four populations. The regressions of the point estimates of recruitment on biomass density displayed strongly significant negative slopes, all within the range of the regressions from the random draws. Models predicting recruitment rates from biomass density 2 months prior were slightly better than models using biomass density 1 month prior. Choice of lag made no difference in CAi, only a small difference in TAt, and a more substantial difference in LLi and ULt.

There were strong seasonal effects of season on recruitment in three of the four populations (LLi, TYt, and ULt; fig. 8; table 3). In those three populations, recruitment was highest in the dry season and lowest in the wet season. The biggest difference was in ULt, in which the average recruitment in the dry season was more than twice the average in the wet season. The differences were substantial, although smaller, in the other two populations. Recruitment rates in CAi were, on average, remarkably similar in all four seasons.

The strong seasonal effects did not remove the strong negative effect of biomass density on recruitment rates

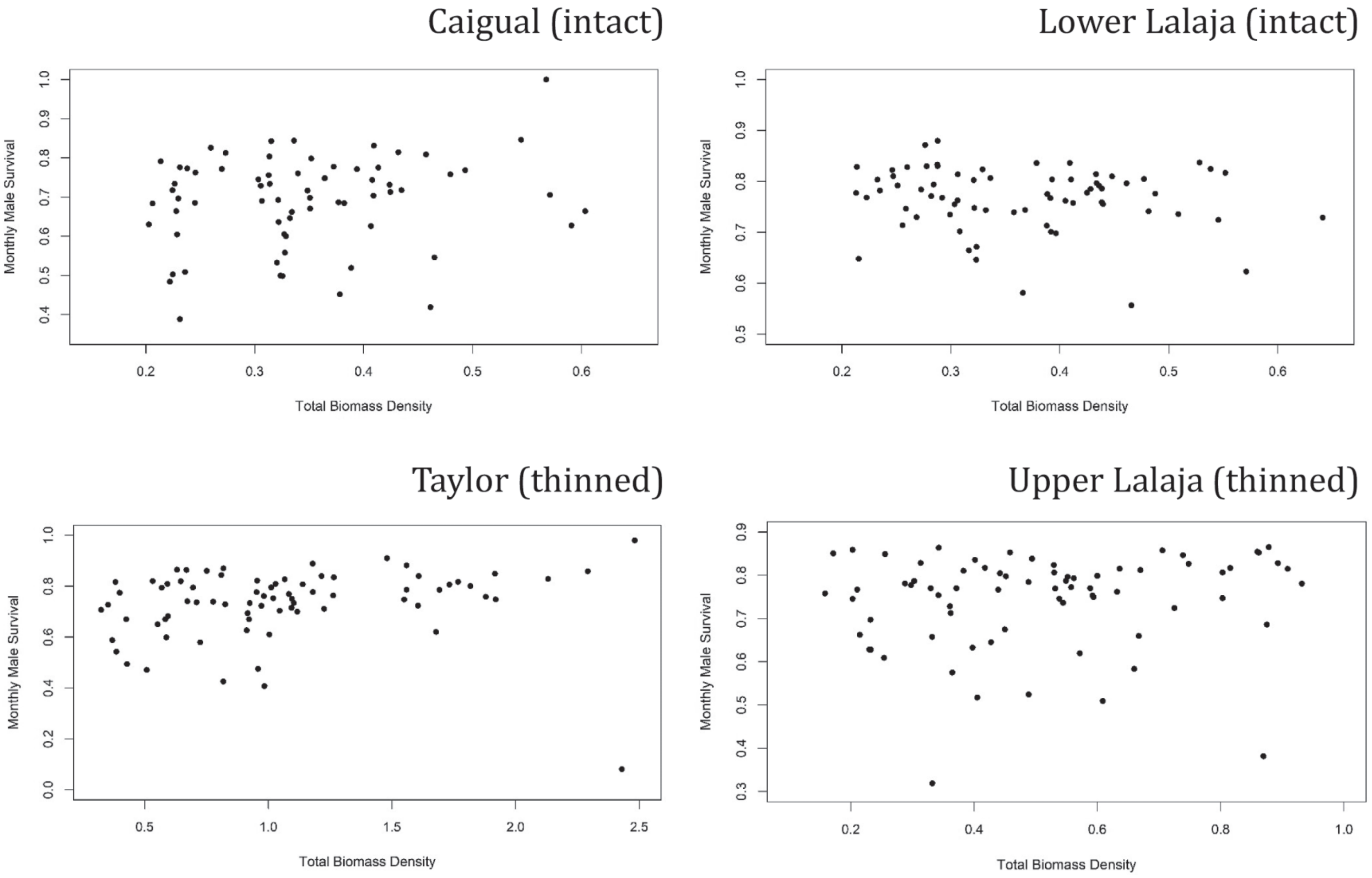


Figure 4: Estimated male survival in each month plotted against total biomass density in preceding month. “Intact” and “thinned” refer to canopy conditions.

Table 2: Results from regressions of demographic variables on total biomass density estimated 1 month and, for recruitment rate, also 2 months previously

Stream and variable	Lower 2.5% bound	Upper 2.5% bound	Regression slope of actual point estimates	Adjusted R^2	Probability that slope equals 0
Caigual (intact):					
Male survival	−.16	1.26	.65	≈0	.30
Female survival	−.26	1.03	.44	≈0	.55
Recruitment and density lag 1	−.79	−.45	−.67	.17	.0005
Recruitment and density lag 2	−.72	−.41	−.62	.16	.0006
Male survival	−.84	−.06	−.46	≈0	.26
Lower Lalaja (intact):					
Female survival	.94	1.70	1.40	.14	.0008
Recruitment and density lag 1	−.59	−.41	−.53	.14	.0007
Recruitment and density lag 2	−.77	−.57	−.71	.26	<.0001
Male survival	.18	.40	.29	.03	.09
Taylor (thinned):					
Female survival	.15	.35	.26	.02	.11
Recruitment and density lag 1	−.28	−.21	−.24	.12	.002
Recruitment and density lag 2	−.30	−.23	−.27	.14	.0005
Male survival	.19	.54	.37	.01	.22
Upper Lalala (thinned):					
Female survival	.53	.84	.69	.06	.02
Recruitment and density lag 1	−.56	−.47	−.52	.22	<.0001
Recruitment and density lag 2	−.56	−.51	−.56	−.26	<.0001

Note: The table includes the lower and upper 2.5% bounds for the slopes of 1,000 regressions, using random draws from the observed monthly distributions of the demographic variable and density. Regressions of male and female survival were performed on logit-transformed values.

(table 3). The slopes of recruitment rate on biomass density were slightly lower in CAi and LLi when season was included as a predictor, but those slopes changed minimally in TAt and ULt. Models incorporating both season and density explained between 27% and 46% of the overall variance in recruitment rates.

Discussion

We found clear evidence for two of the three conditions required for density-dependent selection to be responsible for the evolution of delayed maturity documented in these populations (Reznick et al. 2019*a*; Potter et al. 2021). There was support for regulation of total biomass density in three of our four populations (CAi, LLi, and ULt). Density feedbacks did occur in the fourth (TAt) but not with sufficient strength to keep the population from continuing to grow, albeit slowly. In no population did increased biomass density decrease adult survival; in all four populations, increased biomass density decreased per capita recruitment. These relationships were evident despite strong seasonal effects on both survival and recruitment.

The third condition required by theory is that the life cycle stage at which increased biomass density exerted it strongest negative effect—here, per capita recruitment—must make a major contribution to fitness. We demonstrated that this was so in previous short-term (20–28-day) manipulations of guppy density in natural pools in low-predation habitats (Reznick et al. 2012; Bassar et al. 2013). We found that population growth rates increased when we decreased densities in the pools and decreased when we increased them. Decomposition of those growth rates demonstrated that the survival of juveniles and small adults was the major contributor to growth rate and thus fitness, no matter the direction in which our manipulations changed population growth rate.

While our estimates of per capita recruitment are unknown combinations of adult fecundity and juvenile survival, this makes no difference for generating predictions for the evolution of delayed maturity from traditional density-dependent selection theory. The critical issue is whether increased density decreases fecundity or juvenile survival more than it decreases adult survival (Charlesworth 1994; Engen and Saether 2017). This was the case in these data. It is important to note that this theoretical framework addresses mean density-dependent survival of juveniles relative to mean density-dependent survival of adults. The age-specific effects of density on adult survival

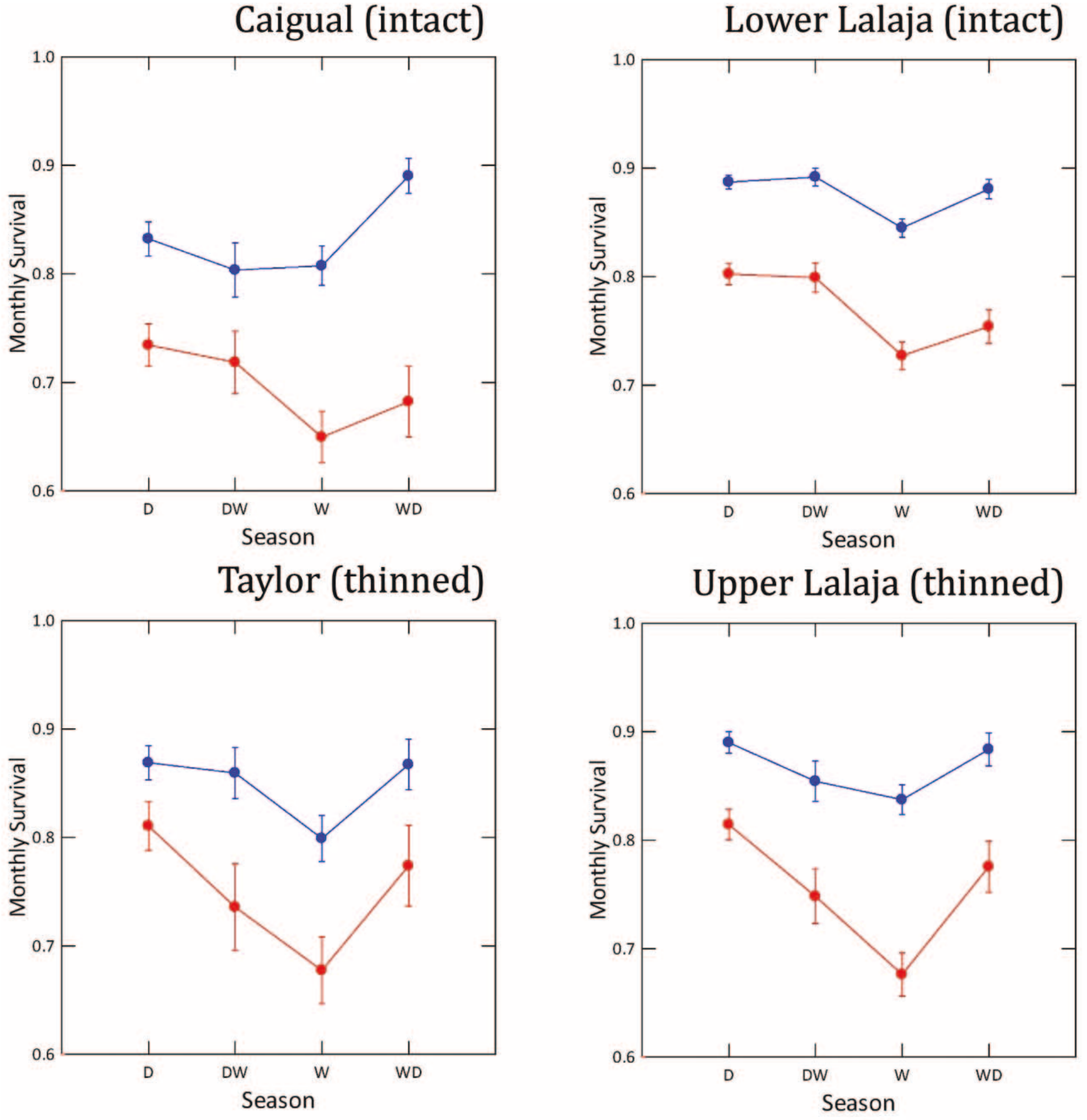


Figure 5: Least squares means of monthly survival of females (blue circles) and males (red circles) from a model using season and biomass density in the preceding month as predictors of logit-transformed survival values. Results are depicted on the back-transformed scale, with standard errors calculated as described in the supplemental PDF.

can have important ramifications for the evolution of senescence (Abrams 1993; Moorad et al. 2019; Roper et al. 2021), a topic beyond the scope of this paper.

There were striking differences in the dynamics of biomass density between the populations under thinned canopies and those under intact canopies. Populations under thinned canopies grew more rapidly after initiation and had higher densities at their peaks than the populations under intact canopies. Populations under thinned canopies had higher densities than typically observed in natural streams, whereas populations under intact canopies had densities similar to those in natural streams (Reznick et al. 2020). The contrast between the biomass densities achieved under intact and thinned canopies supports the

Table 3: Statistical results from ANCOVAs of demographic variables in 1 month as a function of density in either previous month (male and female survival) or 2 months previously (recruitment) and a function of season (dry, dry to wet, wet, wet to dry)

		F		
Stream and variable	Residual df	Season (associated probability)	Density (associated probability)	Adjusted value of R^2
Caigual (intact)	64			
Male survival		2.76 (.05)	.71 (.40)	.13
Female survival		4.12 (.01)	.71 (.40)	.17
Recruitment		1.97 (.13)	14.31 (<.001)	.27
Male survival		9.30 (<.001)	.01 (.93)	.31
Lower Lalaja (intact)	65			
Female survival		7.50 (<.001)	25.16 (<.001)	.37
Recruitment		7.10 (<.001)	13.14 (<.001)	.44
Male survival		4.18 (.009)	5.74 (.02)	.19
Taylor (thinned)	70			
Female survival		2.91 (.04)	3.75 (.06)	.14
Recruitment		4.18 (.009)	5.35 (.03)	.31
Male survival		10.84 (<.001)	6.27 (.01)	.34
Upper Lalaja (thinned)	68			
Female survival		3.61 (.02)	10.03 (.002)	.20
Recruitment		4.98 (.004)	20.87 (<.001)	.46

Note: Canopy treatments for each stream are in parentheses.

hypothesis that under natural (intact) canopies, guppies are resource limited.

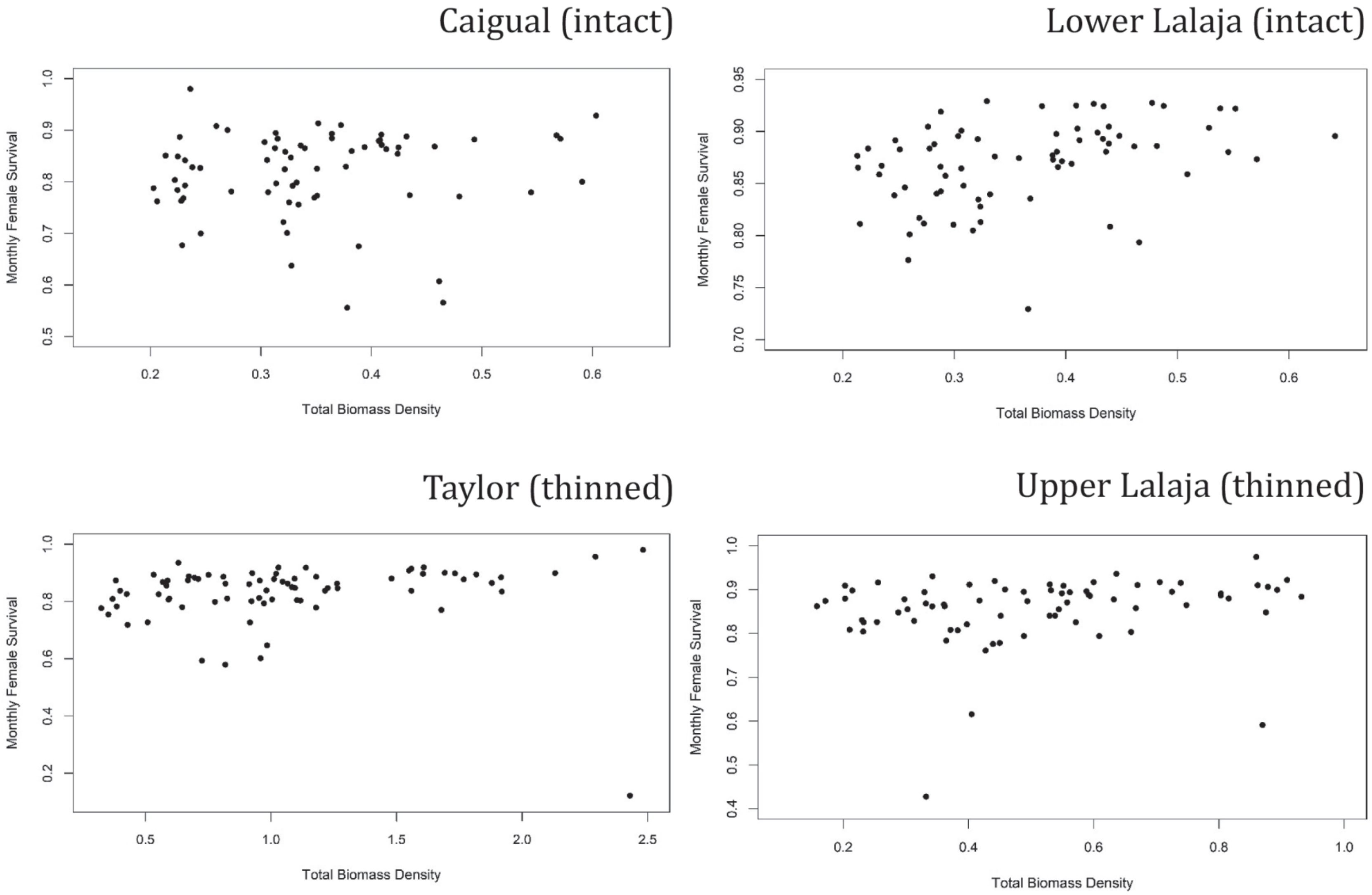
The populations under thinned canopies also displayed larger seasonal fluctuations after the initial growth period. These larger amplitudes reflect differences in the maximum densities achieved; the lowest values within these fluctuations were similar between the two types of populations. These fluctuations between dry and wet seasons reflected the same seasonal fluctuations in adult survival and recruitment rate.

Despite these differences between the populations under thinned and intact canopies, there was no effect of canopy thinning on the timing of evolutionary change in male age and size at maturity in these experimental populations (Reznick et al. 2019*a*). This could reflect the beneficial effect of the higher productivity of these streams in balancing the deleterious effects of increased density. This is especially notable in TAt because its light level was an order of magnitude greater than that of the other thinned stream, ULt (Kohler et al. 2012). This could explain why TAt showed little evidence for regulation and a continued steady increase in density over the period of study.

The key factor in creating the selection pressure for delayed maturation could be the per capita food level. The enhanced productivity in the streams under thinned canopies suggests that per capita food levels may not have been as different between the thinned and intact canopy streams as the differences in their densities might suggest. The crucial issue for both regulation and density-dependent selection is not density per se but the relationship between the productivity of the habitat and the demands made by the population on the habitat's resources (Engen et al. 2020).

The per capita food level for guppies is also affected by the density of the only other fish in these streams, the killifish, *Rivulus harti*, because juvenile and young adult killifish share food resources with guppies (Travis et al. 2014). It is not clear, though, how much killifish contributed to the regulation of these guppy populations. For one reason, killifish densities, especially the densities of smaller killifish, declined substantially following the introduction of guppies and did not return to previous levels in the period of this study (Goldberg et al. 2022). For another, in the size range in which the two species overlap, guppies are the superior competitors (Anaya-Rojas et al. 2021). Thus, at the densities of the two species observed here, intraspecific effects are more likely to be the predominant agent of regulation.

Contrary to expectation, monthly adult survival increased at higher biomass densities in three of the four populations. This pattern was much weaker than the negative effects of biomass density on recruitment, which were evident in all four populations. The pattern also occurred in short-term (28-day) mesocosm experiments (R. D. Bassar, T. Coulson, D. Reznick, and J. Travis, personal observation). There are multiple hypotheses for this pattern, including social facilitation of foraging efficiency (Reader et al. 2003; Wright et al. 2020) and social alleviation of physiological stress (Burford et al. 2019). A more complicated hypothesis is that increased biomass density is associated with a shift in adult age structure toward ages at which fish have higher survival rates. Testing this hypothesis—which requires estimating


Caigual (intact)

Lower Lalaja (intact)

Taylor (thinned)

Upper Lalaja (thinned)

Figure 6: Estimated female survival in each month plotted against total biomass density in preceding month. “Intact” and “thinned” refer to canopy conditions.

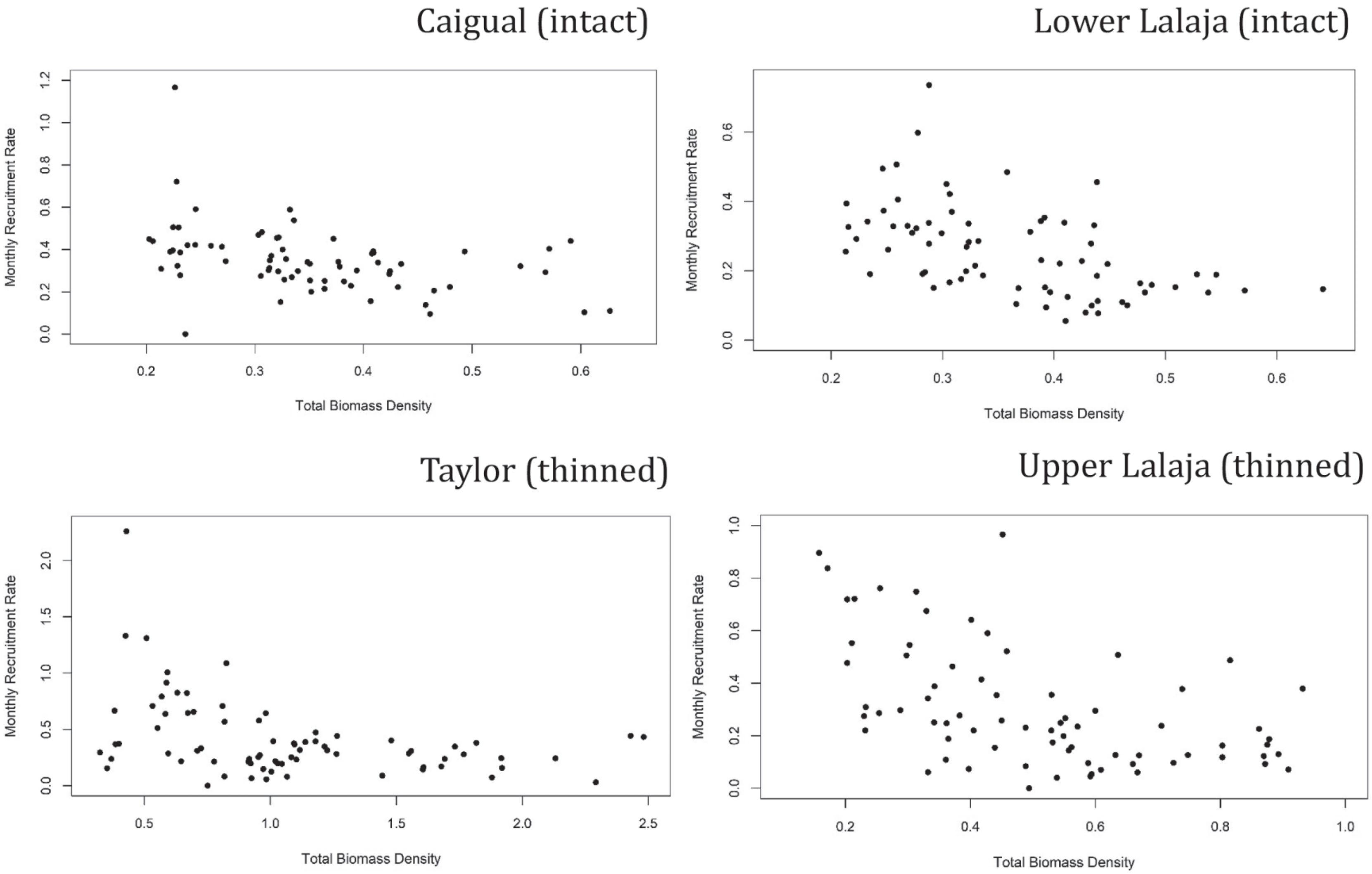


Figure 7: Estimated recruitment rate (recruits per female) in each month plotted against total biomass density 2 months prior. “Intact” and “thinned” refer to canopy conditions.

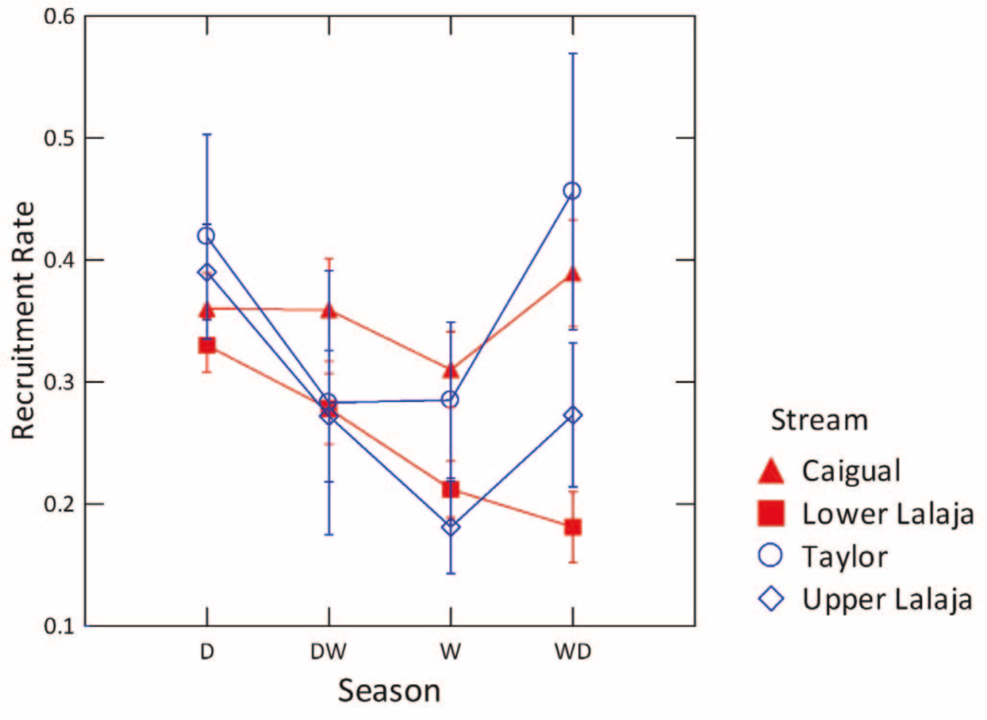


Figure 8: Least squares means of recruitment rate (recruits per female) plotted as a function of season in each stream. Caigual and Lower Lalaja had intact canopies, and Taylor and Upper Lalaja had thinned canopies.

the ages of individual fish from their capture and growth histories—is beyond the scope of this paper.

The results from this long-term experimental study are consistent with the results from our short-term manipulations under intact canopies. It is worth noting that the only other study of which we are aware that compared short-term manipulations and long-term censuses found that the two methods did not agree on the strength of population regulation (Fowler et al. 2006). One difference between our study and Fowler's is that our time series was longer and included very large fluctuations in density, comparable in magnitude to our perturbations (i.e., doubling observed densities and halving observed densities). This may have facilitated the ability of our short-term perturbations to point us in the right direction.

In a larger sense, our results illustrate the critical value of long-term studies (Dodds et al. 2012). By "long term," we mean a study whose duration includes multiple generations. It is critical that any long-term study of regulation and the potential for density-dependent selection measure changes in density over short time steps. Had we done censuses on these populations annually, we could not have obtained the demographic data vital to testing density-dependent selection theory. While rapid evolution is now widely recorded (Reznick et al. 2019*b*), we still need long-term ecological studies to understand how and why such evolution occurs.

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Statement of Authorship

D.R. conceived the idea for the work; D.R. and J.T. designed the study. D.R., R.D.B., and A.L.-S. developed the census methods and the processes for data collection and on-site archiving. All authors participated in obtaining funding for the work; T.C. obtained funding to build the database for the mark-recapture data. R.D.B. curated the data; R.D.B. and J.T. were responsible for quality control of data used in this paper. R.D.B. and J.T. wrote all code used for analyses of these data. All authors contributed to refining ideas, writing, and editing of the manuscript.

Data and Code Availability

Data and code for the analyses in this article are available in the Dryad Digital Repository, https://doi.org/doi:10.5061/dryad.pc866t1rh (Travis et al. 2023).

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“The traveler who enters for the first time a New Zealand forest, no matter from what land he may have wandered, will find everything new and strange to him. . . . The ferns alone number about a hundred and twenty species, and form the most characteristic feature in the landscape. Thousands of these beautiful plants cover the ground with their low and delicate fronds, as in some portions of our own country; others entwine the trunks of trees for support; still others attain the size of forest trees and rear their great crowns of feathery fronds to a height of forty or fifty feet in the air, rivaling in their grace and elegance the date-palm of Arabia.” From “A Sketch of New Zealand with Pen and Pencil” by I. C. Russell (*The American Naturalist*, 1879, 13:65–77).