

# Pulses of marine subsidies amplify reproductive potential of lizards by increasing individual growth rate

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Pulsed resource subsidies can have profound effects on recipient communities. The effects of resource pulses are often mediated by increases in the density of consumer populations. Here we investigate several mechanisms linking experimental pulses of seaweed deposition to population-level responses in the brown anole *Anolis sagrei*. Subsidized lizards grew approximately 30% faster than lizards in seaweed-removal plots, but there was no effect of seaweed subsidies on survival or body condition. Breeding is strongly seasonal in *A. sagrei*, resulting in a limited reproductive window of opportunity. Accelerated growth allows subsidized females to reach sexual maturity earlier and thereby exploit more of this window, which is projected to double fecundity in their first year of life. These results show how changes in an individual trait can translate pulses of resource input into reproductive output. Further, they highlight the importance of seasonal timing in mechanistically linking individual-, population- and community-level responses to pulsed resource subsidies.

Spatio-temporal variation in resource availability is an important determinant of population and community dynamics (Ostfeld and Keesing 2000, Holt 2008). Pulsed resource subsidies are large magnitude increases in resource abundance that occur rarely, are brief in duration, and involve spatial transport of resources across habitat or ecosystem boundaries (Yang et al. 2008). The effects of such pulsed resource subsidies on recipient communities are often mediated by changes in consumer density (Holt 2008). These numerical responses to pulsed subsidies can be associated with both behavioral aggregations and in situ reproductive responses (Ostfeld and Keesing 2000, Baxter et al. 2005, Yang et al. 2008, 2010). In order to achieve a comprehensive and mechanistic understanding of how these numerical responses occur, it is important to link changes in individual life-history characteristics to population-level outcomes. However, few studies of numerical responses to pulsed subsidies include the detailed observations of individuals required to make these connections.

Changes in a number of individual traits can contribute to consumer numerical responses. Increases in growth rate (Sabo and Power 2002, Wipfli et al. 2003, Baxter et al. 2007, Marczak and Richardson 2008, Denton et al. 2009), survivorship (Bergeron et al. 2011), and energy allocated to reproduction (Spiller 1992) can all increase consumer

density in response to pulsed subsidies. The timing of resource pulses relative to consumer phenology may play an important role in determining the mechanism of consumer response and the resulting population and community dynamics (Takimoto et al. 2002). For example, nesting and rearing periods in birds have been shown to coincide with peak aquatic insect emergence (Francis et al. 2006) and forest insect outbreaks (Both et al. 2009), and short-lived consumers may initiate reproduction in anticipation of resource pulses to minimize demographic lags between peak resource abundance and peak consumer abundance (Boutin et al. 2006, Marcello et al. 2008, Bergeron et al. 2011). Thus, a detailed understanding of consumer phenology is a crucial element in studies seeking to gain mechanistic insight into the relationship between individual traits and population responses.

Here we investigated how pulsed marine subsidies affect life-history characteristics of brown anole lizards, *Anolis sagrei*, in shoreline habitats. Seaweed deposition occurs mostly in the fall in this system, although the precise timing and magnitude of subsidies is unpredictable in a given year. In a previous study, we showed that an experimental pulse of fall seaweed deposition caused lizards to switch from foraging on terrestrial prey to consuming seaweed detritivores (Spiller et al. 2010). In addition, lizard densities increased in experimentally-subsidized plots, and higher lizard densities were also observed in sites that naturally receive high subsidies due to favorable currents and

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coastline topography. We hypothesized that increases in density found after the first three months of subsidization were due to immigration into seaweed-addition plots from surrounding areas. However, peak lizard abundance was observed a year after the initial pulse, suggesting that a time-lagged reproductive response also occurred. Breeding is seasonal in *A. sagrei*, and this limited reproductive window of opportunity likely constrains how individuals can respond to seaweed pulses. In the current study, we analyzed morphological and mark–recapture data from lizards over a period of 20 months to determine whether subsidized lizards survived better, had improved body condition, or grew faster than unsubsidized lizards. These results are synthesized with information on the reproductive phenology of *A. sagrei* to determine how changes in individual characteristics could explain long-term increases in population abundance.

## Methods

### Seaweed subsidy experiment

Our study took place in the Exumas, a chain of islands in the central Bahamas. Four 10 × 10 m uncaged plots were established on each of three islands for a total of 12 plots. Islands exceeded 100 000 m<sup>2</sup> in area and each island was treated as a block. Plots were separated by 10–30 m and extended inland from the high-tide line. We are confident that movement of lizards between plots was extremely rare. In similar habitats, *Anolis sagrei* has been observed to move 0.5 to 5 m over successive years, as measured by the distance between home-range centers of recaptured individuals (Schoener and Schoener 1982). In hundreds of lizard recapture events in this study, on only two occasions were lizards recaptured in a plot other than the one in which they were originally marked. Such switching could have been due to lizard movement or human error in releasing lizards post-processing.

Seaweed deposition occurs naturally during the fall at our study sites, so we manipulated seaweed abundance during September and December of 2006 and 2007 to simulate two years of resource pulses. Plots were assigned one of two treatments in a systematically interspersed design (Hurlbert 1984): seaweed added (hereafter ‘subsidized plots’) or seaweed removed (hereafter ‘unsubsidized plots’). The amount of seaweed we added to plots was approximately 2.5 kg m<sup>-2</sup>. In most cases natural seaweed deposition on our study plots was minimal, so the unsubsidized plots were not manipulated. However, on a few occasions some of the unsubsidized plots received approximately 0.5 kg m<sup>-2</sup> of naturally-deposited seaweed – this was removed to maintain target seaweed levels. The amount of seaweed added or removed was based on monitoring data from 29 nearby unmanipulated plots that all naturally supported lizard populations. Average seaweed abundance per plot was 0–2.2 kg m<sup>-2</sup> over a three-year period, with peaks in seaweed abundance approaching 10 kg m<sup>-2</sup> (Spiller et al. 2010, Piovia-Scott et al. 2013). Thus, our manipulation contrasts two realistic target levels of seaweed abundance – high (subsidized) and low (unsubsidized).

Lizards found in the plots were captured by hand or noose during six field trips: September 2006, December 2006, May 2007, September 2007, December 2007 and May 2008. We spent 3–5 consecutive days on each island during sampling trips, resulting in approximately 12 person-hours per plot per trip catching lizards. Our sampling was nearly exhaustive: temporary paint marks indicated that less than 10% of lizards observed on the last day of each sampling trip were unmarked. Lizard snout–vent length (SVL) was measured to the nearest 0.5 mm with a ruler, and mass was measured to the nearest 0.01 g with an electronic balance. Individuals were uniquely marked on all trips except for May 2007. Individuals received two tags of one color and a third tag of a different color. We injected tags into the ventral side of the limbs, using each limb segment as a different tag site for a total of eight possible tag locations. Our data were limited to lizards larger than 27 mm in length because smaller animals are not commonly encountered in the field using visual survey methods (Pike et al. 2008) and are difficult to mark permanently.

### Growth rate

To test for a seaweed subsidy effect on individual growth rate we fit the logistic-by-weight model, which models body size in terms of weight growing logistically to an asymptote. In a review on body size growth in reptiles, Andrews (1982) concluded that the logistic-by-weight model was most appropriate for small, short-lived lizards like anoles. In addition, previous work has found that the logistic-by-weight model provided a better fit for *A. sagrei* growth data than two plausible alternative models across several Bahamian populations (Schoener and Schoener 1978). The interval equation version of the logistic-by-weight model (written in terms of weight proportional to the cube of

length) is:  $L_2 = \left\{ \frac{(a^3 L_1^3)}{L_1^3 + (a^3 - L_1^3)e^{-rD}} \right\}^{1/3}$ . Three variables

are needed to fit the growth model:  $L_1$  = snout–vent length at start of interval,  $L_2$  = snout–vent length at end of interval, and  $D$  = length of the interval in days. Two parameters, the asymptotic size ( $a$ ) and the characteristic growth rate ( $r$ ), are estimated from the model. The characteristic growth rate describes how quickly individuals achieve asymptotic size. The maximum growth rate (i.e. the inflection point) occurs at  $a/1.59$  (Schoener and Schoener 1978).

We used the nlme function in the R package ‘nlme’ to fit logistic-by-weight growth models as non-linear mixed effects models (Pinheiro et al. 2011). The parameter  $a$  varied by sex in all models because males are larger than females at asymptotic size in this species. Preliminary analyses found no effects of the seaweed treatment or island on asymptotic size and no interactive effect of seaweed treatment and sex on characteristic growth rate. Therefore we present results from models where  $a$  varies by sex only and  $r$  varies by sex, treatment, and island. To account for the non-independence of lizards from the same plot and multiple interval measurements from the same lizard, we included plots and individuals as random effects, with individuals nested within plots. We used likelihood ratio (LR) tests to

evaluate the significance of the fixed effects (sex, treatment, and island) in the model. Most lizards were only captured twice, generating a single mark–recapture interval for the growth-rate analysis. For lizards that were caught multiple times, we used each consecutive recapture interval in the model. For example, a lizard marked on trip 1 and recaptured on trips 2 and 3 would generate data for mark–recapture intervals 1 to 2 and 2 to 3, but not 1 to 3.

### Apparent survival

We use the term ‘apparent survival’ because it is not possible to determine whether an animal that is not recaptured has died or has emigrated out of the sampling area. For *A. sagrei*, the frequency of transients (animals present for less than one week) has been estimated as ranging from 0 to 30% in habitats similar to our experimental sites (Schoener and Schoener 1982). The lack of a correlation between percent transients and survival rates in that study lead the authors to conclude that emigration is unlikely to have a large effect on survival estimates, thereby increasing confidence in inferences drawn from our mark–recapture models for *A. sagrei* in the present study.

To evaluate the effect of seaweed treatment on apparent survival, we used the function `F.cjs.estim` from the R package ‘`mr`’ to fit Cormack–Jolly–Seber mark–recapture models assuming closed populations during sampling periods and open populations between sampling periods (McDonald 2012). The `F.cjs.estim` function relates individual capture histories to covariates using a regression approach (Amstrup et al. 2005). We fit models with sex, treatment and island as covariates, and used LR tests for hypothesis testing. As in the growth analyses, preliminary analyses indicated that there was no significant sex by treatment interaction, so this term was dropped from the final model.

### Body condition

Body condition was modeled using a linear mixed-effects model fit with the `lmer` function in the R package ‘`lme4`’ (Bates et al. 2011). Mass was the response variable and SVL, sex, treatment, sampling trip and island were fixed predictor variables. As in the growth models, plot and individuals nested in plots were random effects. Mass in grams and SVL in mm were log-transformed. We initially fit models that included sex-by-treatment and SVL-by-treatment interactions; these interactions were not significant and were dropped from subsequent models. As above, we used LR tests to evaluate the significance of the fixed effects in the model.

### Reproductive phenology and time to maturity

Breeding is seasonal in *A. sagrei*, with the highest frequencies of reproductive females typically occurring from the late spring through summer (Licht and Gorman 1970, Sexton and Brown 1977, Lee et al. 1989, Goldberg et al. 2002, Norval et al. 2012). *Anolis* lizards lay a single egg at a time and are capable of producing an egg every 5–25 days on average (Andrews and Rand 1974), with *A. sagrei* capable of producing an egg every 7–10 days under optimal conditions

during the breeding season (J. Losos pers. comm.). Incubation times are approximately one month (Losos et al. 2003). In populations in southern Florida, those *A. sagrei* nearest to our study sites for which reproductive cycles have been documented, the frequency of reproductive females was highest from April to September, with no reproductive females observed from November to February (Licht and Gorman 1970, Lee et al. 1989). We observed very few small animals during May field trips, which is similar to patterns observed on islands near Abaco, in the northern Bahamas (Schoener et al. 2002). Based on the observed frequency of small animals and reproductive cycle data from other populations, we inferred that the peak egg-laying period at our study sites occurs between May and September.

We used the parameter estimates from the growth model to predict time to maturity for females. We assumed a size at hatching for *A. sagrei* of  $L_1 = 16.5$  mm SVL (Duellman and Schwartz 1958), and that females are sexually mature at a minimum of 34 mm SVL (at least one developing ovarian follicle present; Licht and Gorman 1970). We combined information on predicted time to maturity, the seasonality of peak egg-laying, and the rate of egg production to estimate the reproductive window of opportunity and fecundity for subsidized and unsubsidized females during their first breeding season. These calculations assumed that lizards were born at a constant rate during the peak hatching period (1 June to 1 October 2006), grew at a treatment-specific rate, and produced one egg per week during the peak egg-laying period in 2007 (1 May to 1 September) once they achieved reproductive size.

### Immigration

The observed increases in lizard density in subsidized plots reported in Spiller et al. (2010) could have been due to both immigration and reproduction. We used the growth model to estimate the relative abundance of immigrants as follows. First, we used data from all recaptured lizards to estimate the parameters  $a$  and  $r$  (as described previously). By re-arranging the growth model to solve for  $L_1$  we were able to calculate how large an unmarked animal captured on a given trip was on the previous trip. This calculation was based on the animal’s size at capture ( $L_2$ ), the duration between the time of capture and the time of interest in the past ( $D$ ), and the sex- and treatment-specific parameter estimates for  $a$  and  $r$ . Given our confidence that plots were sampled nearly exhaustively for animals larger than 27 mm SVL, we assumed for this analysis that all lizards larger than 27 mm SVL were captured and permanently marked on each trip. Therefore, if an unmarked lizard was inferred to have been of a detectable size ( $L_1 > 27$  mm SVL) during the previous trip it was classified as an immigrant – had it been a resident during the previous trip it would have been captured and marked. Lizards with an inferred previous trip  $L_1 < 27$  mm SVL were classified as unknown status because they could have been present but missed due to their small size, or they could have immigrated into the plot between trips. Previously marked animals were classified as recaptures (i.e. non-immigrants).

We used the `lme` function in the R package ‘`nlme`’ (Pinheiro et al. 2011) to test whether the number of

immigrants increased in subsidized plots compared to unsubsidized plots. Lizard counts were the response variable in a linear mixed-effects model, and counts (which included zeroes) were square-root transformed to meet assumptions of normality. Lizards were placed into two immigration classes: immigrants, or other (unknown status and recaptured lizards pooled). Immigration class, treatment, sampling trip and island were fixed effects. Plot was a random effect, and the random effect of plot was allowed to differ between immigration classes. Residuals were modeled using a first-order autoregressive structure to account for residual similarity in lizard counts on consecutive sampling trips (Pinheiro and Bates 2000). All interactions between fixed effects were included in preliminary models; LR tests were used to evaluate the significance of fixed effects.

### Age structure

Increases in reproductive output are likely to alter the age structure of a population. To determine whether age structure varied between subsidized and unsubsidized plots, we used the growth model to classify individuals as young-of-the-year based on size. We used the sex-specific parameter estimates for  $a$  and the treatment-specific parameter estimates for  $r$  from the growth model to estimate how large an animal born on 1 April of a given year would be in the middle of our sampling trips during the same year. All animals this size or smaller were classified as young-of-the-year to create an age class variable. While 1 April is earlier than the hatching dates for eggs laid during the peak egg-laying period, this date was chosen to be maximally inclusive for animals born in a given year.

We used the `lme` function in the R package 'nlme' (Pinheiro et al. 2011) to test whether the number of young-of-the-year increased in subsidized plots over time. Lizard counts were the response variable in a linear mixed-effects model, and counts (which included zeroes) were square-root transformed to meet assumptions of normality. Age class, treatment, sampling trip, and island were fixed effects. Plot was a random effect, and the random effect of plot was allowed to differ between age classes. Residuals were modeled using a first-order autoregressive structure to account for residual similarity in lizard counts on consecutive sampling trips (Pinheiro and Bates 2000). All interactions between fixed effects were included in preliminary models; LR tests were used to evaluate the significance of fixed effects.

## Results

### Growth rate

Snout-vent length data from 165 individuals (82 females, 83 males) were used to model body-size growth rate. Most individuals were only recaptured once (73%), but multiple captures for the other animals resulted in a total of 238 growth intervals. Animals in subsidized plots had larger growth rates than unsubsidized animals, growing approximately 30% faster ( $r$  unsubsidized = 0.0083,  $r$  subsidized = 0.0109;  $\chi^2 = 6.46$ , DF = 1,  $p = 0.011$ ; Fig. 1, 2A). Males

and females did not differ in their characteristic growth rates ( $\chi^2 = 1.73$ , DF = 1,  $p = 0.188$ ; Fig. 2A). Asymptotic size for females and males was 42.5 mm and 58.4 mm, respectively (Fig. 1).

### Apparent survival

Capture histories from 486 individuals (193 females, 293 males) were used in the mark-recapture analysis to estimate apparent survival. Females had higher month-to-month apparent survival probabilities on average than males (females: 80%, males: 49%;  $\chi^2 = 25.64$ , DF = 1,  $p < 0.0001$ ; Fig. 2B), but there was no seaweed treatment effect on apparent survival ( $\chi^2 = 1.54$ , DF = 1,  $p = 0.214$ ; Fig. 2B). Most animals were only caught once (66%), including new unmarked animals encountered on the last field trip ( $n = 79$ ). Eight animals were captured on both the first and last trips. Seven of these animals were adults when first captured (six females  $\geq 39$  mm SVL, one male 57.5 mm SVL), suggesting they were at least two years old (and probably closer to three years old) at the end of the study.

### Body condition

Snout-vent length and mass data from 484 individuals (193 females, 291 males) were used to model body condition ( $n = 727$  because of measurements on recaptured animals). Length was a significant predictor of mass ( $\chi^2 = 1815$ , DF = 1,  $p < 0.0001$ ; Fig. 2C). There was no treatment effect on mass ( $\chi^2 = 0.02$ , DF = 1,  $p = 0.888$ ; Fig. 2C), indicating that there was no effect of seaweed subsidies on body condition. Sex had a significant effect on mass ( $\chi^2 = 10.37$ , DF = 1,  $p = 0.001$ ), with males being slightly heavier than females of the same snout-vent length by a factor of 1.04.

### Reproductive phenology and time to maturity

Predicted growth trajectories indicated that seaweed subsidies reduced the age at which female lizards attained reproductive maturity by 81 days (time to maturity: unsubsidized 340.5 days, subsidized 259.3 days). Assuming that eggs are produced at a constant rate throughout the peak egg-laying period, 60% of subsidized females born in 2006 would have been large enough to reproduce for the entire peak egg-laying period in 2007 (1 May to 1 September), and even the latest-hatching animals would have been large enough to reproduce for a minimum of 10 weeks (Fig. 3). In the absence of seaweed subsidies, 5% of unsubsidized females would have missed the 2007 peak egg-laying period altogether, while the earliest-born animals would have missed the first week (Fig. 3). By calculating the mean across individuals representing all 2006 hatching dates, we find the average fecundity of young-of-the-year subsidized females in the 2007 breeding season was more than double that of unsubsidized females: 16.2 versus 7.9 eggs.

### Immigration

There was a significant treatment  $\times$  immigration class interaction, driven by higher numbers of recaptured and unknown-status lizards in subsidized plots (treatment  $\times$



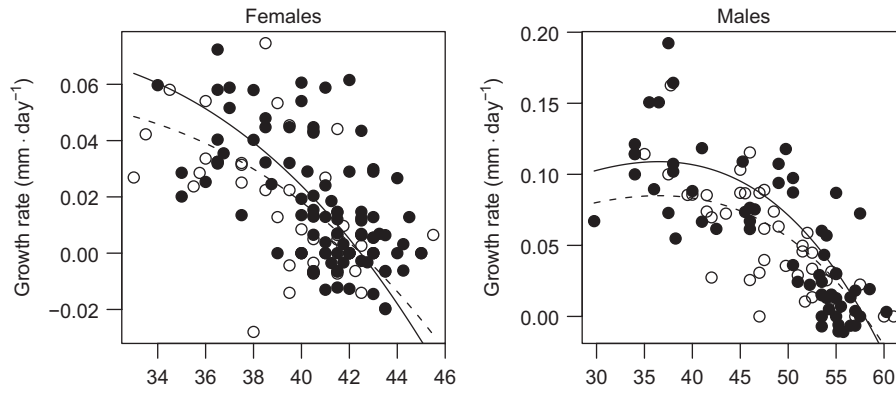


Figure 1. Growth of male and female *Anolis sagrei* in plots with and without seaweed subsidies. Points represent change in snout-vent length ( $L_2 - L_1$ ) over time (days) by average snout-vent length  $(L_1 + L_2/2)$  for each lizard recapture interval used in the study. Lines represent predictions from the logistic-by-weight model. Filled symbols and solid lines represent subsidized lizards, open symbols and dashed lines represent unsubsidized lizards. Where the two lines cross at  $Y = 0$  is the estimate of asymptotic size.

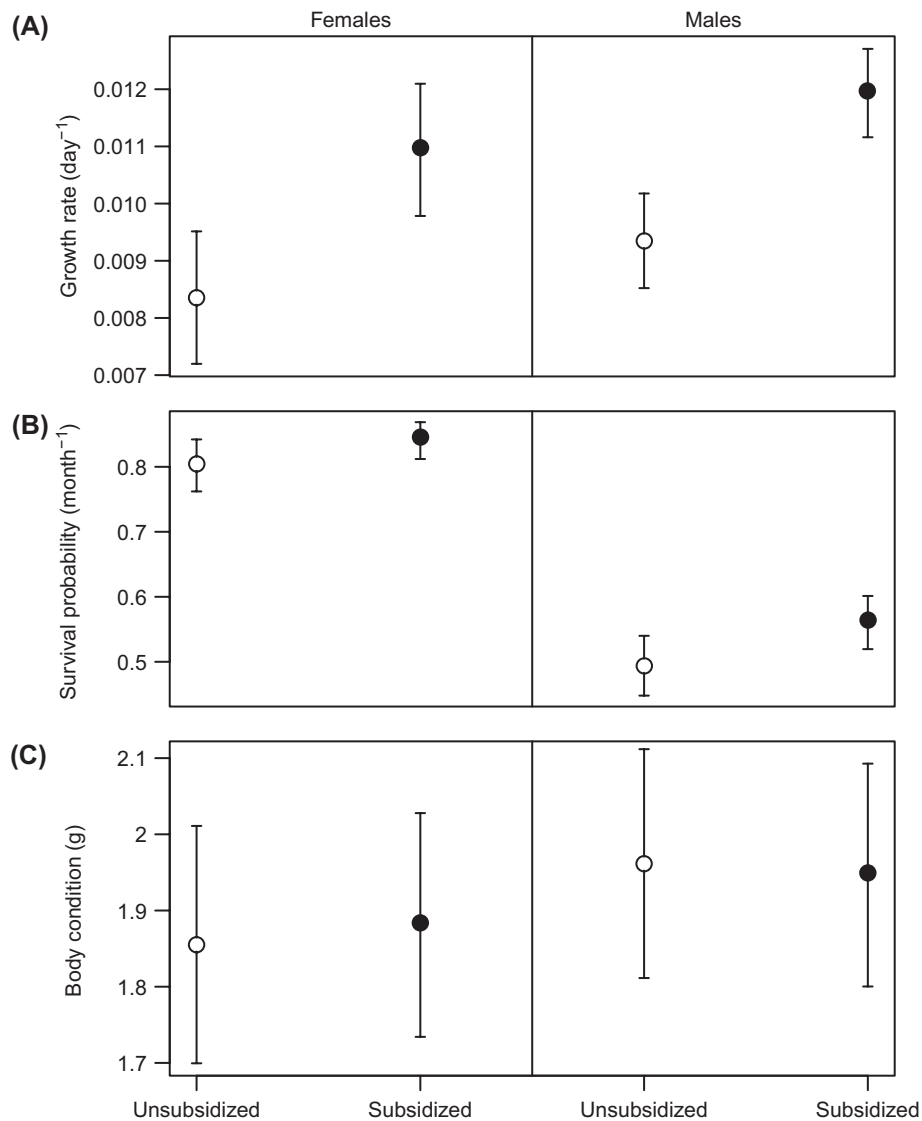


Figure 2. Effect of seaweed subsidies on lizard traits. Filled symbols represent subsidized lizards, open symbols represent unsubsidized lizards. Error bars are model-estimated standard errors. (A) Growth rate: characteristic growth rate ( $r$ ) estimates from the logistic-by-weight-model. (B) Survival: monthly apparent survival probability estimates from the Cormack-Jolly-Seber mark-recapture model. (C) Body condition: model-estimated mass.

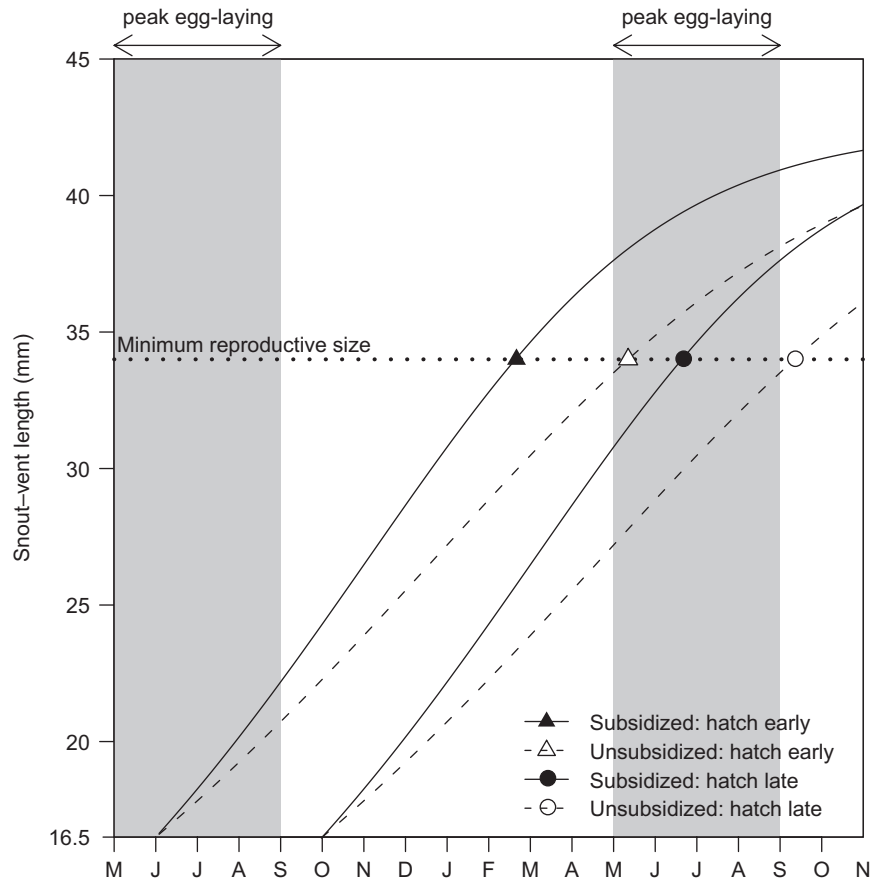


Figure 3. Estimated growth and reproductive phenology for females born during the study period. This scenario assumes a size at hatching of snout-vent length = 16.5 mm, a one-month incubation time, and that the peak egg-laying period is from May to September (shaded boxes). The dotted line indicates minimum reproductive size (snout-vent length = 34 mm). Growth trajectories follow lizards hatching early (June) and late (October) in the breeding season. Symbols (triangles and circles) mark when lizards reach minimum reproductive size depending on hatch date and whether seaweed was added (solid lines) or removed (dashed lines).

immigration class  $\chi^2 = 4.44$ ,  $DF = 1$ ,  $p = 0.035$ ; immigrants subsidized vs unsubsidized contrast  $F_{1,18} = 1.37$ ,  $p = 0.257$ ; other subsidized versus unsubsidized contrast  $F_{1,18} = 17.20$ ,  $p < 0.001$ ; Fig. 4). Thus, there is no indication that there

were more immigrants in subsidized plots – rather, there were more lizards that could not be classified as immigrants (unknown status and recaptured lizards) in subsidized plots than in unsubsidized plots.

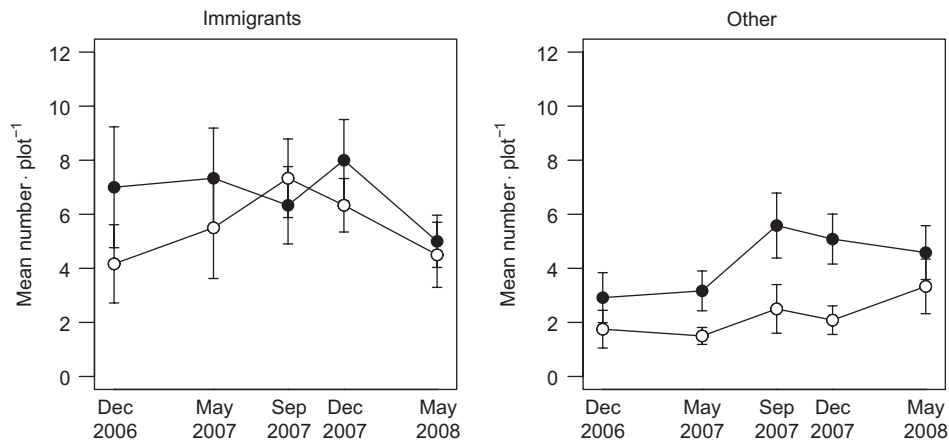


Figure 4. Mean numbers of immigrants versus other (i.e. recaptured and unknown status) lizards in unsubsidized (open symbols) and subsidized (filled symbols) plots. Note that September 2006 is not shown because all animals were new and unmarked at the beginning of the study. Error bars are standard errors.

## Age structure

The difference between the abundance of young-of-the-year and non-young-of-the-year animals in subsidized and unsubsidized plots varied over time (treatment  $\times$  age class  $\times$  sampling trip:  $\chi^2 = 17.29$ ,  $DF = 1$ ,  $p = 0.004$ ; Fig. 5). Independent contrasts between seaweed treatments within trips showed that there were more young-of-the-year animals in subsidized than unsubsidized plots in September and December 2007 (September:  $F_{1,12} = 5.03$ ,  $p = 0.045$ ; December:  $F_{1,12} = 7.42$ ,  $p = 0.018$ ; Fig. 5).

## Discussion

Pulsed subsidies can increase consumer populations through multiple mechanisms. Here we show that pulses of marine subsidies increased the growth rate of lizards in shoreline plots, providing females the opportunity to lay more eggs during their first year of life. While short-term increases in lizard density in response to pulsed seaweed subsidies may largely be driven by aggregation (Spiller et al. 2010), our results suggest that long-term increases are partly driven by increased reproductive output of younger lizards, which is enhanced by the seasonal correspondence between seaweed deposition and lizard reproductive phenology.

In the present study, we estimated that accelerated time to maturity doubles fecundity for subsidized young-of-the-year females compared to unsubsidized females. Constraints on the reproductive window of opportunity underlie this effect – the breeding season is limited, and the time it takes a female to reach reproductive size determines how much of that period is available in her first year. For lizards that hatched early, both subsidized and unsubsidized females reached reproductive size before or near the start of the peak egg-laying period and therefore could have produced similar numbers of eggs over the season (Fig. 3). At the other extreme, a subsidized female that hatched at the end of the breeding season in the fall would have reached reproductive size in time to reproduce throughout more than half of her first breeding season (Fig. 3). In contrast, that same female in

the absence of subsidized resources would grow more slowly and be unlikely to breed at all in her first year; this female would need to survive until the next breeding season in order to reproduce, roughly 10 months after the subsidized female laid her first egg (Fig. 3).

Two additional pieces of evidence support the proposition that increased reproduction is driving long-term population increases. First, there was no indication that the abundance of immigrants was higher in subsidized plots than in unsubsidized plots, while there was evidence that the abundance of other classes of lizards was higher in subsidized plots (Fig. 4), suggesting that long-term increases in density in subsidized plots were not associated with increased immigration. Second, the number of young-of-the-year animals increased in subsidized plots over time, peaking in year two of the experiment (Fig. 5). This increase in young-of-the-year lizards is consistent with a one-year lag in reproductive response due to animals born in situ reaching reproductive size sooner and contributing additional offspring in year two of the experiment.

The patterns in growth rate and survival documented in this study are consistent with data from previous studies on *Anolis sagrei*. The parameter estimates for  $a$  and  $r$  reported here fall within the range of values reported by Schoener and Schoener (1978) in an observational study on Bahamian *A. sagrei*. They found that growth rate was positively associated with lizard density and hypothesized that this was because density was higher in sites with more food. Our results support this interpretation, as we documented increases in both lizard density and growth rate in response to experimentally increased prey abundance (Spiller et al. 2010, this study). The absence of an increase in apparent survival due to subsidy is consistent with the idea that predation is likely the major source of mortality for anoles (Schoener and Schoener 1982, Schoener et al. 2005). Schoener and Schoener (1982) showed that female *A. sagrei* have higher survival than males, as we found here, and hypothesized that this was because males defend territories using conspicuous visual displays that make them more susceptible to predation risk.

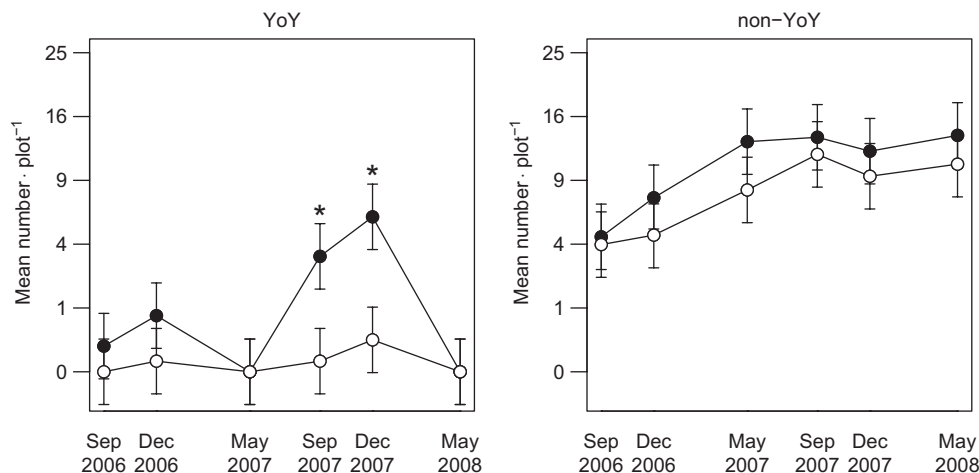


Figure 5. Model-estimated mean number of lizards captured in unsubsidized (open symbols) and subsidized (filled symbols) plots on each sampling trip: (A) young-of-the-year, (B) non-young-of-the-year. Error bars are model-estimated standard errors. \*  $p < 0.05$ .

In a meta-analysis, Yang et al. (2010) found that consumers with combined aggregative and reproductive responses showed greater and more persistent responses to resource pulses than consumers responding by either mechanism alone. In this system, aggregative responses likely occur relatively quickly (weeks to a few months), whereas reproductive responses result in a one-year time lag between peak resource abundance and peak consumer abundance. In an observational study, we found that lizard densities were higher in unmanipulated sites that naturally receive high seaweed deposition than in sites with naturally low deposition (Spiller et al. 2010). Such persistent effects on population size could be facilitated by the reproductive response described here combined with aggregative responses. The time lag in achieving peak lizard abundance may also have contributed to community-level food web effects. During the period of peak subsidized prey (i.e. seaweed detritivore) abundance, lizards shifted from eating terrestrial prey to subsidized prey, resulting in increased plant damage by terrestrial herbivores (a negative indirect effect of seaweed on plants). However, because of the lagged reproductive response, high lizard abundance persisted after the prey subsidy declined and lizards switched back to eating terrestrial herbivores (Spiller et al. 2010). Persistently high lizard abundance likely acted to suppress herbivores and prevent plant damage over a longer time scale (a positive indirect effect of seaweed on plants). A comparative study of sites naturally receiving chronic seaweed subsidies documented that this indirect pathway does indeed occur (Piovia-Scott et al. 2013). Thus, delayed reproductive responses by lizards help explain changes in the indirect effects of pulsed subsidies on plant damage over time.

Our results underscore the importance of the timing of resource pulses with respect to consumer phenology in determining the mechanism and magnitude of their effects (Yang et al. 2008, Takimoto et al. 2002). Pulses of seaweed deposition usually occur after or near the end of the egg-production period in this system. As a consequence, little opportunity exists for adults to directly invest seaweed-derived energy into eggs. While changes in *A. sagrei* body condition have been documented in other field experiments, (e.g. in response to experimental predator addition, Schoener et al. 2002), the lack of an increase in body condition in subsidized lizards in the present study suggests that they are not storing resources for future use. Instead of benefitting from increased growth (as they are already near asymptotic size), storage, or survival, subsidized adults may take advantage of seaweed pulses by spending less time foraging when prey is abundant and easy to catch. The relative strength of such behavioral shifts in influencing population dynamics is an interesting question for further study in our and other systems. Thus, resource pulses occurring early in development drive increased population size by allowing juveniles to reach sexual maturity earlier, while individuals receiving subsidies late in development receive little direct benefit.

Juveniles also represent an important mechanistic link between the timing of resource pulses and consumer responses in other systems as well. In a study of riparian spiders, Marczak and Richardson (2008) found that resource pulses occurring late in development increase

juvenile growth rate, body condition, and the speed of reproductive development more than resource pulses occurring early in development. In another example, Bergeron et al. (2011) found higher juvenile survival and population growth for chipmunks in years with large pulses of beech seed availability, but no difference in adult survival. In this case, the consumer uses anticipatory reproduction to adjust its phenology to match the timing and magnitude of the resource pulse – in years with no beech seed available, chipmunks did not reproduce at all prior to seed set. Formulating a conceptual framework to better understand how the timing of a resource pulse affects juvenile growth and survival would be a fruitful next step in advancing the study of resource pulses.

Our study documents a link between the timing of resource pulses and the ability of consumers to exploit limited reproductive windows of opportunity. Understanding these types of linkages is crucial in our rapidly-changing environment – climate change can affect both consumer phenology (Parmesan 2006) and the timing and magnitude of resource pulses (Yang et al. 2008, 2010), and the consequences of these changes for communities and ecosystems will depend on the degree to which consumer densities are affected. Hence, by elucidating the mechanisms underlying consumer responses to resource pulses, we can gain insight into basic ecological questions as well as the complex consequences of climate change.

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