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Abstract

Increases in consumer abundance following a resource pulse can be driven by diet shifts, aggregation, and reproductive responses, with combined responses expected to result in faster response times and larger numerical increases. Previous work in plots on large Bahamian islands has shown that lizards (*Anolis sagrei*) increased in abundance following pulses of seaweed deposition, which provide additional prey (i.e., seaweed detritivores). Numerical responses were associated with rapid diet shifts and aggregation, followed by increased reproduction. These dynamics are likely different on isolated small islands where lizards cannot readily immigrate or emigrate. To test this, we manipulated the frequency and magnitude of seaweed resource pulses on whole small islands and in plots within large islands, and monitored lizard diet and numerical responses over four years. We found that seaweed addition caused persistent increases in lizard abundance on small islands regardless of pulse frequency or magnitude. Increased abundance may have occurred because the initial pulse facilitated population establishment, possibly via enhanced overwinter survival. In contrast with a previous experiment, we did not detect numerical responses in plots on large islands, despite lizards consuming more marine resources in subsidized plots. This lack of a numerical response may be due to rapid aggregation followed by disaggregation, or stronger suppression of *A. sagrei* by their predators on large islands in this study. Our results highlight the importance of habitat connectivity in governing ecological responses to resource pulses and suggest that disaggregation and changes in survivorship may be underappreciated drivers of pulse-associated dynamics.

Introduction

Resource pulses can reveal ecological connections across organizational scales from individuals to ecosystems (Ostfeld and Keesing 2000, Yang et al. 2008). A key link between individual- and population-level effects of resource pulses is the consumer-response mechanism (*sensu* Yang et al. 2010; e.g., Ostfeld and Keesing 2000, Sears et al. 2004). Important response mechanisms include changes in what consumers eat (diet shifts), where they eat (habitat use), and how they use what they eat (i.e., how they allocate resources to growth, maintenance, and reproduction). Diet shifts by resident consumers can occur rapidly (e.g., McCormick 2003, Kenny et al. 2017), and the aggregation of non-resident consumers into subsidized areas can increase local consumer density faster than reproduction can (Yang et al. 2010). However, aggregating individuals can track resource fluctuations across space and time (e.g., Sanchez-Ruiz et al. 2018), limiting the duration of local numerical responses. These mechanisms are not mutually exclusive, with combined aggregative and reproductive response generating the largest numerical responses (Yang et al. 2010).

The degree of habitat connectivity may influence the interaction between consumer-response mechanism and numerical responses by limiting the ability of consumers to aggregate and disaggregate rapidly. For example, Gratton and Denno (2003) found that nitrogen pulses had the biggest food-web effects when predators were able to respond aggregatively in continuous habitats. The impact of resource pulse frequency and magnitude (e.g., Takimoto et al. 2009, Leroux and Loreau 2012) may also depend on habitat connectivity. Larger magnitude pulses generally result in larger consumer responses (Yang et al. 2010), but these effects may be delayed, reduced, or both if aggregation is limited by habitat isolation. Repeated pulses over time can result in compounding effects on consumer abundance (e.g., Leroux and Loreau 2012; Gratton et al. 2017). Such carryover effects may be stronger in isolated habitats where

disaggregation is weak, allowing populations to build up over time, though ecosystem size will likely constrain carrying capacity.

The timing of resource pulses with respect to consumer life history, seasonal phenology, and colonization events can also influence consumer response mechanisms (Marczak and Richardson 2008, Wright et al. 2013). For example, Sato et al. (2016) found that resource pulses resulted in demographic responses during the summer, but not when pulses occurred in the fall. Resource pulses that occur during resource-limited periods could be particularly important for the persistence or establishment of populations. This idea is related to the “Fluctuating-resource Hypothesis”, which posits that plant communities are more susceptible to the establishment of new species when there is an increase in the availability of unused resources, as during a resource-pulse event (Davis et al. 2000). While this general hypothesis has been evaluated in plant communities (e.g., Davis and Pelsor 2001, James et al. 2006) and microbial communities (e.g., Li and Stevens 2012), it is unclear to what degree pulsed resources are likely to affect the establishment of animal populations.

Seaweed deposition on shorelines in the Bahamas provides an opportunity to explore consumer responses to different resource-pulse regimes in isolated vs. continuous habitats. While background deposition occurs tidally, brief pulses of high seaweed deposition are associated with storms in the fall, and deposition among nearby local sites can vary across several orders of magnitude (Spiller et al. 2010, Figs. S2-S3). A key consumer in this system is the brown anole lizard (*Anolis sagrei*, hereafter lizards), a generalist predator of small invertebrates. Decomposing seaweed supports detritivores, providing an ephemeral source of alternative prey that assembles following seaweed deposition and dissipates over time as the pulse attenuates (Spiller et al. 2010). The food-web consequences of seaweed pulses occur via an above-ground

pathway driven by lizard behavioral and numerical responses: lizards switch from resident prey to subsidized prey, then increase in abundance and switch back to terrestrial prey, causing herbivory to increase then decrease over time (Spiller et al. 2010). There is also a below-ground pathway by which decomposing seaweed fertilizes plants, increasing herbivory in chronically subsidized areas (Spiller et al. 2010, Piovia-Scott et al. 2013). Focusing on the consumer response mechanisms, lizards shifted to consuming seaweed detritivores within three months of subsidy, and the diet shift peaked then attenuated within a year (Spiller et al. 2010). A numerical response occurred within three months due to aggregation (Spiller et al. 2010), and after one year due to reproductive responses (Wright et al. 2013).

These previously reported responses to seaweed pulses have been documented on large Bahamian islands ($>10^4$ m², hereafter mainlands), where lizards are able to move between habitat patches. We aimed to take advantage of the natural distribution of lizards on small and large islands to test how isolation may affect consumer responses to pulsed subsidies. Responses to seaweed pulses may be different on small islands ($<2,000$ m²) because they are isolated and undergo rapid turnover. Isolation limits the ability of lizards to aggregate and disaggregate, with small islands receiving immigrants much more rarely than movements between patches on mainlands. In addition, small islands undergo population turnover (i.e., extirpation and recolonization) on ecological timescales due to hurricanes (e.g., Spiller et al. 1998, Schoener et al. 2001, Schoener et al. 2004, Kolbe et al. 2012), and therefore populations on small islands differ from mainlands in repeatedly undergoing establishment dynamics. While island size likely determines other aspects of ecological context besides isolation and colonization history, we have drawn on extensive prior research in this system to account for and minimize other sources

of variation through careful selection of study islands, randomization, and measurement of *a priori* covariates.

Here we compare the effects of different resource-pulse regimes on lizard diet and abundance in two habitat types: large mainland islands with resident lizard populations vs. small islands with newly-established lizard populations. We applied three different seaweed addition treatments for comparison with controls (no seaweed added) over four years: 1) a single large resource pulse; 2) several large resource pulses; 3) several small resource pulses (with total deposition of small pulses over the whole study equal to one large pulse). This design allows us to parse the effects of resource pulse timing and magnitude by comparing the effect of seaweed addition relative to controls across different treatments (e.g., Piovia-Scott et al. 2019). For example, a timing effect can be determined by comparing effect sizes between “single large” and “several small”, as the total magnitude of added seaweed is the same while the timing is all in one pulse (“single large”) vs. spread across three pulses (“several small”). While it was not the primary goal of the current study, this design also allows us to repeat large pulses on mainlands, as in Spiller et al. (2010). Based on resource pulse theory, we predicted that: 1) larger pulses will result in more rapid and more prolonged diet responses than smaller pulses, but timing and duration will be similar in both habitat types; 2) larger pulses will elicit larger, more rapid numerical responses in lizards on mainlands because they are able to respond through both aggregation and reproduction; 3) repeated subsidy events will result in larger consumer population gains on small islands over time due to carryover effects.

Methods

Study system

Our study site is a network of islands along the coast of Great Abaco, Bahamas (Fig. S1A-B). Large amounts of pelagic and benthic macrophytes such as brown algae (e.g., *Sargassum fluitans*) and sea grasses (e.g., *Thalassia testudinum*) are washed ashore in the fall following tropical storms and cold fronts (Spiller et al. 2010). These pulsed subsidies fertilize terrestrial vegetation (e.g., *Conocarpus erectus*), and support a detritivore community (e.g., amphipods, *Tethorchestia* spp., and dipterans; Spiller et al. 2010). Lizards consume prey supported by terrestrial carbon sources (e.g., terrestrial herbivores such as Coleoptera and Lepidoptera) and prey supported by marine carbon sources (e.g., seaweed detritivores such as amphipods). Lizard reproduction is seasonal, with the highest frequencies of reproductive females observed during the wetter period in the late spring and summer, and peak juvenile abundance in the fall (Licht and Gorman 1970, Lee et al. 1989, Wright et al. 2013).

Experimental Design

We used 16 whole small islands plus 20 unenclosed study plots on mainlands as experimental units (Fig. S1B). The 16 small islands were unoccupied by lizards at the start of our study. Small islands were selected at random from a larger pool of 32 islands with suitable habitat, many of which had lizard populations in the past. Small islands were blocked into four size classes (i.e., blocks represent island size, not geographic proximity) prior to assigning seaweed treatments. Each block included four islands, and each island within a block was randomly assigned one of the four seaweed treatments. Island size was measured as the extent of vegetated area because some small islands have rocky areas that are unsuitable for lizards (small island size range: 4-134 m²; see Piovia-Scott et al. 2017). We used five different mainland islands. Each mainland island

served as a block containing four plots (5 blocks x 4 experimental units per block = 20 plots total), and each plot within a block was randomly assigned one of the seaweed treatments. Plots were 10-m wide and extended from the shoreline 5 m into the terrestrial habitat (plots are within the range of sizes of the small islands: area = 50 m², vegetated area range 26.9 – 49 m²). Plots were at least 20 m apart as in Spiller et al. (2010), which is much greater than typical year-to-year movements in this species in similar habitat (0.5 to 5 meters over successive years; Schoener and Schoener 1980).

Pulsed subsidy treatments

We manipulated the timing and magnitude of experimental seaweed additions to create four pulsed subsidy treatments: “control” (no seaweed added), “single large” (one large magnitude pulse in year one), “several small” (small magnitude pulses annually in years one through three, cumulatively totaling the same as the “single large” treatment), and “several large” (large magnitude pulses annually in years one through three, cumulatively tripling the magnitude of the “single large” treatment). The amount of seaweed added per m² of vegetated area for each treatment was determined based on previous data, with large pulses (2.5 kg/m²) similar to natural deposition following storm events, and small pulses (0.83 kg/m²) similar to typical background deposition (Spiller et al. 2010, Piovia-Scott et al. 2011). All experimental resource pulses were added during the period of greatest typical natural seaweed deposition (September-December), with the precise date depending on seaweed availability. Seaweed additions were composed of naturally occurring macrophytes as described above and were in addition to natural background deposition. We documented natural deposition (described below) on all units for inclusion in statistical models (Figs. S2-S3).

Lizard treatments

All mainland plots had resident lizard populations prior to the study. We added adult lizards to 16 lizard-free small islands to control for variation among small islands in recent colonization history. Lizard colonists were collected from a single site on Great Abaco, ~10 km from our experimental units. This approach is commonly used in this study system in order to take advantage of small islands as natural experimental units to study a wide range of topics in ecology, evolution and behavior (e.g. Kolbe et al. 2012, Schoener et al. 2017, Lapiedra et al. 2018). The target stocking density was 0.2 lizards per m² of vegetated area with a 2:1 sex ratio of females to males (mean density 0.22 ± 0.15 , range 0.15 – 0.71; Schoener and Schoener 1980). To ensure the viability of our introduced lizard populations, during the first 1.5 years we added lizards when repeated visits during a sampling period suggested that the population had declined below a mating pair. After the first 1.5 years we allowed populations to go extinct. These re-introductions were minimal (usually one male) and involved small and/or control islands (Table S1). Preliminary analyses showed that reintroductions did not cause populations to increase overall, and the effect of reintroduction on abundance was not considered further.

Timeline

We added lizards to small islands in May 2012. We sampled experimental units three times a year (May, September/October, December) from May 2012 through May 2016. We initiated the seaweed treatments in September 2012, but Hurricane Sandy passed directly over our study area in October 2012, completely washing away the seaweed and lizard treatments, though leaving vegetation cover intact. We re-established treatments by adding new colonist lizards to small

islands and new seaweed deposits to islands and mainlands in December 2012. The “single large” treatments did not receive any additional subsidies after December 2012. The “several small” and “several large” treatments received additional subsidies in the next two years (2013 and 2014), for a total of three subsidy events.

Data Collection

Covariates

To account for biologically relevant differences among experimental units (i.e., each small island or each mainland plot), we measured lizard habitat availability (measured as vegetation volume) and natural seaweed deposition. We expected that experimental units with greater vegetation volume would support larger lizard populations. We estimated vegetation volume as the product of the vegetated area and the average vegetation height on each experimental unit, and barring disturbance this value does not vary substantially over the time scale of the study. We estimated vegetated area visually (see Piovia-Scott et al. 2017). To measure vegetation height, we placed transects 1.5 meters apart and parallel to the longest axis of each unit. At 1-meter intervals, we measured the maximum height of vegetation within a 50-cm radius, and calculated the average of these values for each unit (similar to Kolbe et al. 2012). Seaweed deposition naturally varies in space and time, and locations with more natural seaweed deposition can have higher lizard density and more marine derived diets (Spiller et al. 2010). During each sampling period, we visually estimated the mass in kg of naturally deposited seaweed on each experimental unit following the methods in Spiller et al. (2010). For each experimental unit we used the average of all values collected over the entire study for that unit as a covariate because there was little natural deposition relative to treatments (range kg per sampling period: natural 0-28,

experimental 0-200) and experimental units were consistently ranked by amount of natural deposition received (Figs. S2-S3).

Lizard diet

We used stable isotope analysis to evaluate the percentage of marine-derived carbon in lizard diets. Lizards that consume more seaweed detritivores have higher $\delta^{13}\text{C}$ values because $\delta^{13}\text{C}$ is relatively enriched in marine vs. terrestrial producers (Peterson and Fry 1987, Anderson and Polis 1998). This has previously been verified in our system, where $\delta^{13}\text{C}$ of seaweed is higher than $\delta^{13}\text{C}$ of terrestrial plants, and seaweed addition leads to increased lizard $\delta^{13}\text{C}$ (Spiller et al. 2010, *unpublished data*). All samples were processed by the University of California, Davis Stable Isotope Facility.

We collected approximately 1 cm of tail tissue from 1-3 individual lizards per experimental unit during each sampling period, which previous work has shown is sufficient for determining local population responses to subsidy due to low variation in $\delta^{13}\text{C}$ among co-occurring individuals (Spiller et al. 2010). Tail tissue $\delta^{13}\text{C}$ is indistinguishable from whole body $\delta^{13}\text{C}$ in this species (Takimoto et al. 2008). Lizard sex and body size (snout-vent length) were recorded for each lizard sampled. Lizard samples were kept refrigerated in the field, frozen within 1-8 h, and dried at 55°C to constant mass. We applied a mathematical correction for lipid content based on C:N ratio following Post et al. (2007; Fig. S4). All isotopic samples used in analyses were collected without preservative. Samples collected from the colonists used to populate small islands in December 2012 were stored in ethanol, and ethanol-corrected values (see Fig. S5) are plotted in Figure 1 to visualize initial conditions.

To determine baseline $\delta^{13}\text{C}$ values, we collected samples of seaweed (mainly *Sargassum* spp.) and two common terrestrial plants (*Conocarpus erectus* and *Jacquinia keyensis*). Seaweed samples were collected during each sampling period except September 2014 and were acid fumigated to remove mineral carbonates (Fig. S6). For terrestrial baseline, we collected 10 leaves of *C. erectus* from 1-3 marked focal plants on each experimental unit during each sampling period. We also collected 10 leaves per plant from *J. keyensis* during each sampling period starting in December 2013. Plant tissue was pressed, dried at 55°C to constant mass, and then cryoground under liquid nitrogen to a fine powder and homogenized (seaweed $n = 58$; *C. erectus* $n = 1,566$; *J. keyensis* $n = 320$). Note that the larger sample sizes for terrestrial plants are to document changes in herbivory reported elsewhere (Piovia-Scott et al. 2019).

To determine the fractionation of carbon across trophic levels, we collected samples from terrestrial herbivorous arthropods from every experimental unit during each sampling period. Arthropod samples were refrigerated in the field, frozen within 1-8 h, dried at 55°C to constant mass, cryoground under liquid nitrogen to a fine powder, and homogenized prior to analysis ($n = 618$).

We used a simple mixing model to convert the raw $\delta^{13}\text{C}$ values from lizards, herbivorous arthropods, marine producers, and terrestrial producers to an estimate of the percentage of carbon in lizard diets from marine sources (Post 2002): $100(\delta^{13}\text{C}_L - 2\Delta_C - \delta^{13}\text{C}_T) / (\delta^{13}\text{C}_S - \delta^{13}\text{C}_T)$, where $\delta^{13}\text{C}_L$, $\delta^{13}\text{C}_T$, and $\delta^{13}\text{C}_S$ are the mean carbon isotope ratios for lizards, terrestrial plants, and seaweed, respectively. We used the difference between the mean $\delta^{13}\text{C}$ values for herbivorous arthropods (unpublished data) and the mean $\delta^{13}\text{C}_T$, 1.53, as our measure of Δ_C , the trophic fractionation of carbon.

Numerical response

As an index of lizard abundance, we conducted surveys on each experimental unit during every sampling period starting in September 2013. On each survey, 1-3 observers would search for lizards for 5-27 minutes, with average search effort 22.9 ± 4.0 person-minutes per survey (mean \pm SD). We use the term “abundance” hereafter to refer our index: number of lizards seen per person-minute. Every lizard seen was marked with non-toxic latex paint to ensure each individual was only counted once per survey; paint was applied by using a household spray bottle from a distance of approximately 1 meter. We assume that paint marks are retained throughout a survey because they are only lost when an animal sheds its skin. We recorded life stage (adult vs. juvenile) because sex and body size are difficult to estimate without capturing animals. Each experimental unit was surveyed at least once per sampling period.

Use of an abundance index, in this case, the number of lizards marked per person-minute, assumes that the relationship between the index and actual abundance is the same across space and time (Nichols 1992). While true abundance estimation necessary to test this assumption was not logistically feasible, during October 2015 we conducted our standard surveys on a single day, followed a week later by two weeks of intensive spray-marking on small islands. Each small island was visited on 3-9 days. The number of lizards seen per person-minute during the surveys was correlated with the total number of lizards marked during the more intensive marking effort (Pearson's product-moment correlation: 0.73, 95% CI 0.36-0.90; slope of the log-log relationship: 1.08 ± 0.18 SE, Fig. S7). We assume that this relationship is similar on mainlands.

Data Analysis

Data and R code are available in the Dryad Digital Repository (Wright et al. 2020, <https://doi.org/10.5061/dryad.c2fqz6156>). We used mixed-effects models (Bates et al. 2015, R Core Team 2017) to test whether lizards in different subsidy treatments showed shifts in the diet contribution of marine- vs. terrestrial carbon over the course of the study. The response was the percent marine contribution from the mixing model, which was highly correlated with raw $\delta^{13}\text{C}$ from lizard tail tissue ($r^2 = 0.97$, Figs. S8-S9), and visualization of Q-Q plots and residual vs. fitted plots confirmed assumptions of normality for all models. Seaweed treatment (“control”, “single large”, “several small”, “several large”) and experimental unit type (small islands vs. mainlands) were included as fixed effects, as well as their interaction. Fixed effects were included to account for variation among experimental units in the availability of lizard habitat (vegetation volume), ambient seaweed deposition (mean kg deposited across sampling periods), sex (male vs. female), and body size (snout-vent length). Random effects were included for sampling period, experimental unit (to account for the non-independence of repeated measurements of the same experimental unit over time), and block. To test whether lizards on small islands vs. mainlands showed similar temporal responses to seaweed subsidy, we included interactions between seaweed treatment, experimental unit type, and sampling period as random effects (Bates et al. 2015). Hypothesis tests were conducted using likelihood-ratio tests.

We used a similar mixed-effects modelling approach to test whether lizards in different subsidy treatments changed in abundance over the course of the study. We included the same fixed effects for seaweed treatment, experimental unit type, vegetation volume, ambient seaweed deposition, and the same random effects for experimental unit, block, sampling period, and the same interactions with sampling period. Instead of sex and snout-vent length, we included a fixed effect for stage (adult vs. juvenile), as well as the three-way interaction between stage,

seaweed treatment, and experimental unit type. The response was the number of lizards seen during a survey, which we modeled using a Poisson distribution, an offset to capture the effort over which counts were collected (i.e., log-transformed person-minutes), and an observation-level random effect to account for overdispersion (Crawley 2007, Gelman and Hill 2007, Harrison 2014, Bates et al. 2015). Results are the same if effort is used as a predictor instead of an offset (supplemental model code, Dryad Digital Repository <https://doi.org/10.5061/dryad.c2fqz6156>). We included a random effect for each experimental unit by sampling period combination to account for repeated surveys of the same experimental unit during a given sampling period, and a random factor for day to reflect similarities among surveys conducted on the same day. To account for expected differences in adult and juvenile abundance over time (Wright et al. 2013), we also included a random effect for the interaction between sampling period and stage.

For both the abundance and diet models, we used parametric bootstrap (Bates et al. 2015) to visualize the fitted effects and to calculate effect sizes (mean log response ratio calculated as $\log(\text{treatment/control})$).

Results

Diet

The data set for the diet analysis was composed of 669 lizard-tail tissue samples. We plotted raw data from an additional 122 lizard-tail tissue samples collected prior to subsidy to visualize the initial diet conditions across treatments (sampling period September 2012 for mainlands, December 2012 for islands; Fig. 1). The model testing the effect of seaweed

treatment on marine signature in lizard diets had a marginal r^2 of 0.33 and a conditional r^2 of 0.59 (conditional r^2 reflects the variance explained by the fixed and random effects combined, marginal reflects just the fixed component; Nakagawa and Schielzeth 2013, Bartoń 2017).

The effect of seaweed addition on lizard diet varied on small islands vs. mainlands (*seaweed treatment*experimental unit type*, $\chi^2 = 9.9$, $df = 3$, $p = 0.019$, Figs. 1, 2a): on mainlands, lizard diet in all subsidized plots showed increases in marine signature, whereas on small islands an increase in marine signature was only observed in response to the largest and most frequent pulses (“several large”, Fig. 2a). The baseline marine contribution to diet was higher on small islands than mainlands: percent marine diet (mean \pm SD) for “control” treatments on small islands $36.4\% \pm 0.02$ vs. mainlands $24.0\% \pm 0.01$ (Fig. 1, S9).

The effect of seaweed pulses on lizard diet varied over time (*seaweed treatment*sampling period*, $\chi^2 = 52.2$, $df = 1$, $p < 0.0001$), with the largest response seen in the “several large” treatment following the second subsidy event in September 2013 (Fig. 1). This effect persisted longer on small islands than on mainlands (Fig. 1), likely driving the significant interaction between experimental unit type and sampling period (*experimental unit type*sampling period*, $\chi^2 = 9.0$, $df = 1$, $p = 0.003$). The three-way interaction between seaweed treatment, experimental unit type, and sampling period was not statistically significant ($\chi^2 = 0.19$, $df = 1$, $p = 0.7$); all hypothesis tests are reported from the model without this three-way interaction.

The individual-lizard level covariates (sex and size) were statistically significant, though had small effects. Males had slightly more marine diets than females (model-estimated percent marine contribution to diet: females 32.7%, $n = 352$; males 35.8%, $n = 317$; $\chi^2 = 13.3$, $df = 1$, $p <$

0.001). Smaller lizards had slightly more marine diets than larger lizards: snout-vent length ranged from 23 to 54 mm (mean \pm SD: 40.0 \pm 6.4), and model-estimated percent marine varied from 36.8% to 32.0% across this size range ($\chi^2 = 5.0$, df = 1, p = 0.03). Both of the experimental unit-level covariates showed expected trends with regards to marine signature (though neither of these trends were statistically significant): the marine contribution to diet declined as vegetation volume increased ($\chi^2 = 2.6$, df = 1, p = 0.11), and increased as ambient seaweed deposition increased ($\chi^2 = 3.1$, df = 1, p = 0.08).

Numerical response

We recorded 1,288 lizard sightings during 8,383 person-minutes of surveys. The model exploring the effect of seaweed treatment on lizard abundance had a marginal r^2 of 0.09 and a conditional r^2 of 0.27, thus we have less ability to explain variation in abundance than in diet (this is not surprising when modeling count data as a Poisson process with low numbers).

Lizards on small islands showed a trend towards a larger numerical response to seaweed subsidy than lizards on mainlands (*seaweed treatment*experimental unit type*: $\chi^2 = 7.5$, df = 3, p = 0.057; Figs. 2b, 3, S10). Populations on three out of four “control” small islands declined below a male-female pair within the first 1.5 years of the experiment, and despite reintroductions, populations on the two smallest “control” islands (vegetated area < 14 m²) were not detected on surveys after the first 2.5 years. More adults per person-minute were observed on small islands than in mainland plots (*experimental unit type*stage*: $\chi^2 = 8.8$, df = 1, p = 0.003; Figs. 2b, 3). We observed a significant interaction between stage and sampling period ($\chi^2 = 170.5$, df = 2, p < 0.001), with juveniles present September-December but rare in May (Figs. 3b, 3d). No other interactions with sampling period were statistically significant, indicating that we

did not detect changes in the numerical response over time. The three-way interaction between seaweed treatment, experimental unit type, and stage (juvenile vs. adult) was not statistically significant ($\chi^2 = 1.9$, $df = 3$, $p = 0.59$); neither was the interaction between seaweed treatment and stage ($\chi^2 = 1.6$, $df = 3$, $p = 0.66$; Figs. 2b, 3).

The number of lizards seen per person-minute was positively associated with vegetated volume, approximately doubling from units with the least to the most terrestrial habitat (*vegetated volume*: $\chi^2 = 6.2$, $df = 1$, $p = 0.013$). Natural seaweed deposition was not associated with lizard abundance (*ambient seaweed deposition*: $\chi^2 = 0.02$, $df = 1$, $p = 0.89$).

Discussion

Timing and magnitude of diet shifts

Consistent with expectations, the timing of initial diet shifts was similar on small islands and mainlands. Diet shifts occurred rapidly and were detected at the first post-subsidy sampling opportunity available for each island type. On mainlands, a diet shift was starting to occur by December 2012, suggesting that lizards consumed subsidized prey provided by the initial September 2012 pulse even though it was washed away approximately a month later by Hurricane Sandy (Fig. 1b). Thus, a pulse of seaweed subsidy that was only present for one month resulted in a diet shift that was still detectable three months later. This is consistent with carbon turnover rates documented in similarly-sized lizards (15-91 days depending on tissue type; Warne et al. 2010, Lattanzio and Miles 2016). The first post-subsidy sampling period is May 2013 for small islands because of the hurricane disturbance. Lizards in the “several large”

treatment were clearly differentiated by this time, though it is unclear why “single large” small islands did not respond similarly in the first year (Fig. 1a).

Ecological field studies rarely have multi-year durations or replication over multiple years, but when they do, year-effects are common (Vaughn and Young 2010, Stuble et al. 2017) and can provide insight into un-manipulated factors that affect experimental outcomes. We documented the largest diet shifts after the second subsidy on both islands and mainlands, and this year effect may have been driven by rainfall. Precipitation immediately following the second subsidy (October to December 2013) was similar to the 1977-2016 long-term mean, while the next year (2014) had the fewest rainfall days on record (Figs. 1, S9-10). Wetter conditions in 2013 could have allowed large detritivore populations to build because wet seaweed supports higher detritivore abundance than dry seaweed (*pers. obs.*). The year effect also shows that the hurricane did not confound our island-mainland comparison: if there had been an effect of the “double” subsidy we would have seen the largest diet and numerical responses on mainlands in year one. Instead we saw the largest diet responses on islands in year two and no numerical responses on mainlands.

The magnitude of the diet shift increased with resource pulse magnitude in general as expected; however, diet shifts were seen in all treatments on mainlands but only the “several large” treatment on small islands. This pattern could have emerged because the baseline lizard diets on small islands were highly marine (controls were 1.5 times more marine on small islands than mainlands), possibly obscuring diet shifts in the “single large” and “several small” treatments. Thus, while we assume that lizards on small islands in low-magnitude treatments were consuming seaweed detritivores (which is consistent with the observed numerical responses), if this predation was compensatory (i.e., switching from preying on resident marine

consumers to subsidized marine consumers) then there would be no detectable shift in marine vs. terrestrial diet composition. Subsidized lizards could be obtaining the same percentage of carbon from marine sources yet still benefitting from seaweed pulses if subsidized prey differ in factors such as search time, handling time, quality, etc. In a meta-analysis, Marczak et al. (2007) found that consumer numerical responses were higher in systems with a high ratio of subsidies to equivalent in situ resources, and a similar phenomenon may be occurring here with regards to the diet shift, whereby we only see strong diet shifts when use of in situ marine resources is low.

Timing and magnitude of numerical responses

By comparing the numerical response on isolated small islands vs. plots on mainlands, we aimed to test experimentally whether larger responses are seen when aggregative and reproductive responses are both operating (which could occur on mainlands but not small islands). The patterns we observed were opposite from expected: populations on subsidized small islands showed trends towards increased abundance while populations on mainlands showed no numerical response. We suggest three, non-exclusive hypotheses to explain these unexpected results (while acknowledging that transplantation itself may have unknown effects that impact the interpretation of the island-mainland comparison). First, we hypothesize that the numerical response on small islands was due to resource pulses facilitating establishment of our experimentally introduced populations (“Subsidized-establishment Hypothesis”). Second, the lack of numerical responses observed on mainlands could have resulted if the lizards that rapidly aggregated to use these transient pulsed subsidies subsequently moved out of subsidized plots before our next observation period (“Rapid-disaggregation Hypothesis”). Alternatively, or in

addition, the lack of numerical responses by lizards on mainlands could reflect greater predation pressure on lizards on mainlands than small islands (“Predator-suppression Hypothesis”).

The “Subsidized-establishment Hypothesis” posits that transient periods of increased resource availability following resource pulses creates windows of opportunity that provide colonizing populations with improved prospects for overcoming barriers to establishment. Three pieces of evidence support the idea that it was difficult for lizard populations to establish in the absence of subsidies: 1) populations on “control” small islands declined over time; 2) most “control” island populations went extinct while no subsidized island populations did; 3) populations on subsidized islands were consistently larger than “control” islands during every sampling period regardless of subsidy (Figs. 3a-b, S10). Winters are dry in this system, particularly on small islands, which rely on rain for freshwater and largely lack soil to hold moisture. We introduced adult lizards to small islands in December, and the presence of additional food and/or water retention provided by seaweed may have helped more adults survive over the harsh winter period until the start of the breeding season in the spring. This idea is consistent with seasonal patterns in abundance observed here and in previous studies (Fig. 3, Wright et al. 2013): adults decline during the stressful window in the winter, and their numbers increase in the spring because surviving juveniles from the previous reproductive period transition to adulthood.

We did not see numerical responses to subsequent subsidy events on small islands, suggesting that the initial pulse had larger effects than subsequent pulses. This was particularly striking in the “single large” treatments, as these islands maintained elevated populations despite only receiving subsidies in the first year (Fig. 3). Thus, we suggest that pulsed resources may help colonizing individuals overcome a resource limitation threshold for population

establishment, consistent with the Fluctuating-resource Hypothesis (Davis et al. 2000). Such threshold effects of resource pulses have been observed in other systems (e.g., Yee and Juliano 2011). However, once established, we speculate that the lizard populations in our current study did not respond numerically to subsequent pulses because these small islands were unable to support additional lizards due to other constraining factors (e.g., space, habitat features).

For the mainlands, we propose two non-exclusive explanations for the lack of observed numerical responses: lizard movement out of subsidized plots, and predation. The “Rapid-disaggregation Hypothesis” suggests that local numerical responses occurred on a shorter time scale than we were able to detect by sampling three times a year. We have observed that lizards undergo short-term habitat shifts on the scale of minutes to days to forage in seaweed on the ground (Kenny et al. 2017). Lizards may also be making brief sorties into subsidized plots and then rapidly returning to the surrounding habitat. In addition, juveniles born inside of mainland plots are able to disperse out of them. Thus, while there may be short-term aggregative movements into plots and increased reproduction due to seaweed resources, there may also be movements out of the plot by adults and juveniles when subsidized prey decline, or to escape high lizard densities. Following the short- and long-term movements of marked individuals would be necessary to test this hypothesis.

Limitation by predators is another general mechanism by which prey populations could be prevented from responding numerically to increased resource availability. There are several cases where prey populations only increased in response to resource supplementation when predators were also excluded (e.g., Huitu et al. 2003, Haapakoski et al. 2012, Krebs et al. 2018). Top-down control has also been proposed to limit consumer responses to resource pulses (e.g., Weber et al. 2018). Levi et al. (2015) developed predator-prey models where resource pulses

increased prey carrying capacity, and found a range of outcomes including the scenario where predators suppressed numerical responses by prey. No predators of our focal species were resident on small islands, while we saw several predatory species on mainlands such as snakes (Bahamian racers, *Cubophis vudii*) and curly-tailed lizards (*Leiocephalus carinatus*). Curly-tailed lizards can affect the abundance, behavior, habitat use, and morphology of our focal lizard species (Schoener et al. 2005, Lopez-Darias et al. 2012, Schoener et al. 2017, Lapiedra et al. 2018). In addition, small islands did not support nesting bird predators, and they likely receive fewer visits from predatory birds than mainland plots.

Repeatability of ecological field experiments

Large field experiments are rarely repeated in ecology, and it is striking that we generally corroborated the results of our previous study regarding the timing and magnitude of diet shifts, but not the results regarding the numerical response. In the previous study (Spiller et al. 2010), we applied a large resource pulse to six plots on three mainland islands and monitored the food web for one year. If we consider the first year of the current study, we applied the same magnitude resource pulses to 10 plots on five mainlands (because the “single large” and “several large” treatments are the same in year one). Thus we repeated and expanded the previous study but the numerical response of the previous study was not observed: Spiller et al. (2010) found large numerical responses while the current study found none.

We speculate that substrate and rainfall differences between the sites may at least partially explain differences in the numerical responses observed in these two experiments. The previous experiment took place in the central Bahamas in the Exumas, while we conducted the current study in the northern Bahamas (Great Abaco) because of the availability of small islands.

In the Exumas, populations in sandy beach habitat had larger numerical responses than populations on rocky shorelines. The Great Abaco islands are composed of dark rock, which may be warmer and thereby restrict lizard activity and movement (i.e., aggregation and disaggregation). Substrate type may also affect retention of seaweed-derived nutrients. Although the Exumas are generally more xeric than Abaco, the study there was conducted in years with above average rainfall days (2006-07) compared to the current experiment where rainfall days tended to be below average (2012-16, Fig. S11). The effects of rainfall on these food webs is likely complex, but may affect baseline levels of terrestrial prey availability. If terrestrial prey populations decline in dry years, then subsidized prey may not be sufficient to promote population gains. In studies of the effect of lizards on spiders, the relationship between interaction strength and rainfall was flipped from positive in the drier Exumas to negative in the wetter Abaco region (Spiller and Schoener 2008), showing that climatic variability can have a large effect on trophic interactions in this system.

We designed the current experiment specifically to test expectations from a robust conceptual and empirical framework in a well-studied system, and ultimately were unable to confirm many of those expectations. While we lack data to support our *a posteriori* explanations, we present them as hypotheses to be tested in future work. In repeating aspects of a prior study, we replicated the strong diet shifts on mainlands but not the numerical response, suggesting that whether additional resources translate into additional individuals is highly context-dependent (Subalusky and Post 2019). These results underscore the need to grapple with the issue of reproducibility in ecology (Schnitzer and Carson 2016), something that our field's focus on novelty often discourages.

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Author Contribution Statement

LHY, TWS, and JPS acquired the funding. All authors contributed to the methods and experimental design. ANW, JPS, LHY, and DAS collected the data. ANW led the data analysis and wrote the original draft. All authors contributed to review and editing.

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Figure Legends

Figure 1. Lizard diet shift in response to pulsed subsidies over time on a) small islands and b) mainlands. The y-axis is the percent of the diet contributed from marine sources estimated from $\delta^{13}\text{C}$ stable isotope analysis. Circles are fitted effects from a parametric bootstrap of the lizard diet model described in the text ($\pm 95\%$ CI). Pre-subsidy values (diamonds) were calculated from raw data (mean $\pm 95\%$ CI). Points are jittered for visualization. Solid gray bars indicate when experimental seaweed pulses occurred. The dashed gray bar indicates the initial seaweed pulse that was subsequently wiped out by Hurricane Sandy in October 2012.

Figure 2. Overall effect of seaweed pulse treatments on lizard a) diet and b) abundance. Effect sizes are the log response ratio $\pm 95\%$ CI calculated using the fitted effects from the parametric bootstrap of the diet and abundance model, respectively. The log response ratio was calculated as $\log(\text{treatment}/\text{control})$, such that a value of 0 indicates no treatment effect, positive values indicate more marine diets or greater abundance in treatments compared to controls, and vice versa. Effect sizes were calculated within experimental unit types (e.g., single large islands compared to control islands).

Figure 3. Lizard numerical response to subsidy on small islands (a, b) and mainlands (c,d); the top row shows adults (a,c), while the bottom row shows juveniles (b,d). The y-axis is the estimated number of lizards seen per 24 person-minutes of survey effort. Points are fitted effects from a parametric bootstrap of the lizard abundance model described in the text ($\pm 95\%$ CI). Points are jittered for visualization. Solid gray bars indicate when seaweed pulses occurred. The

dashed gray bar indicates the initial seaweed pulse that was subsequently wiped out by Hurricane Sandy in October 2012

Figure 1

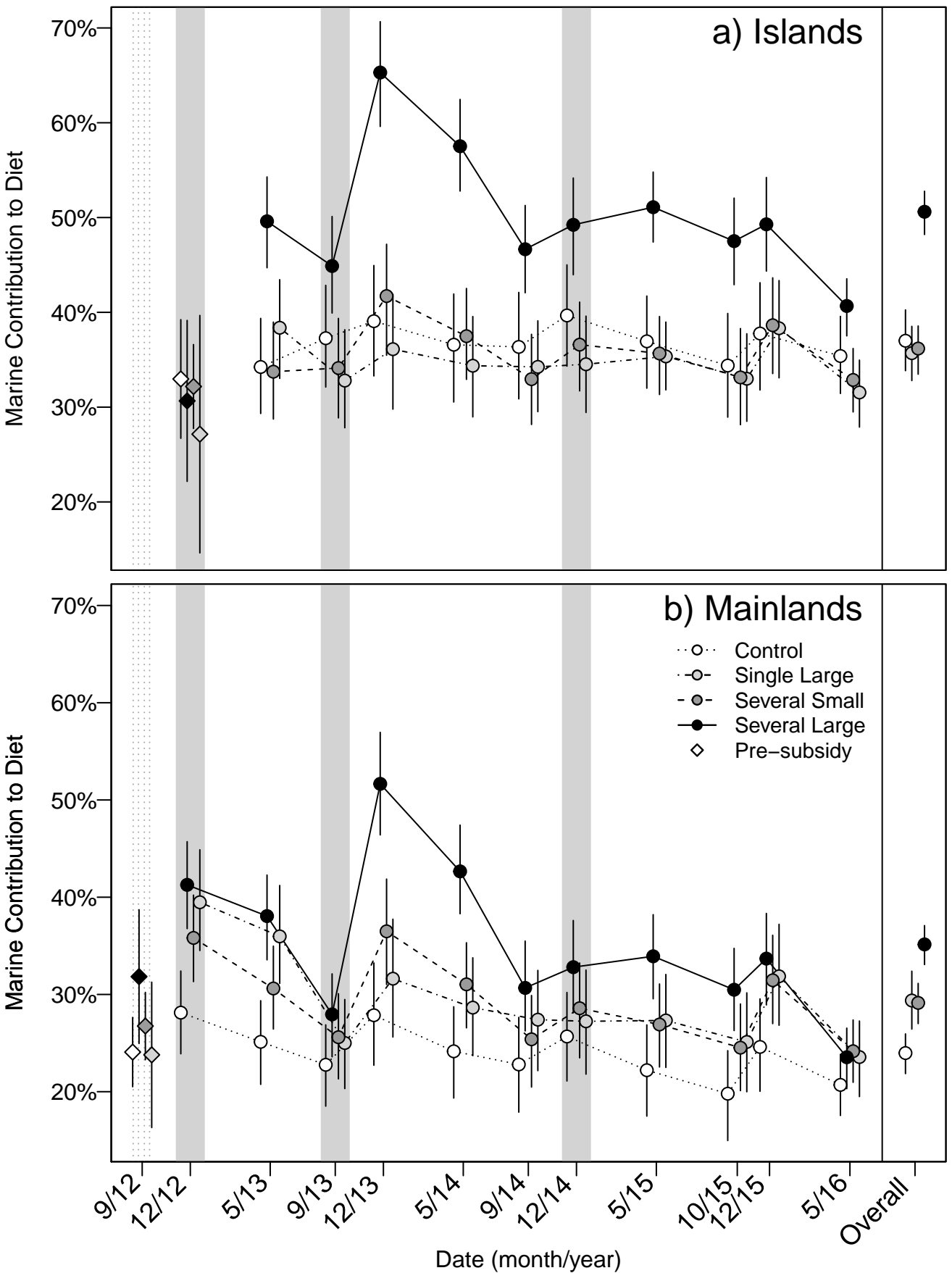
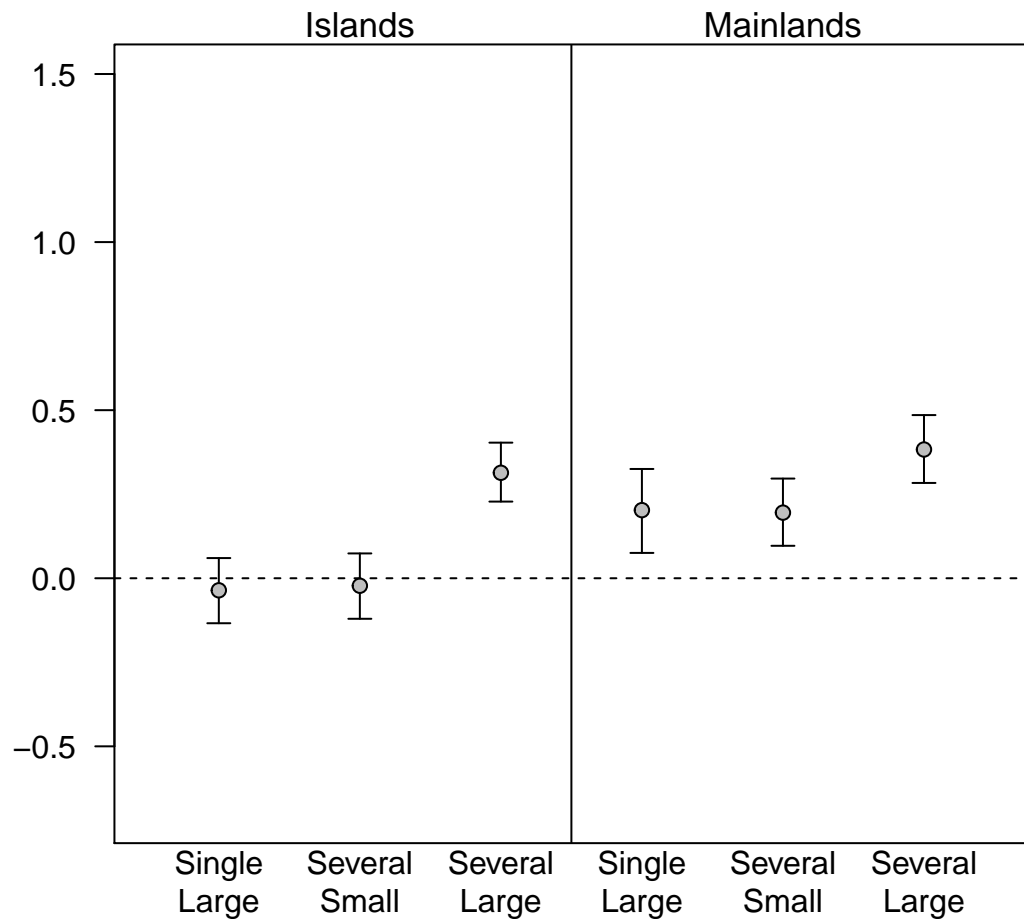


Figure 2

a) Diet Response



b) Numerical Response

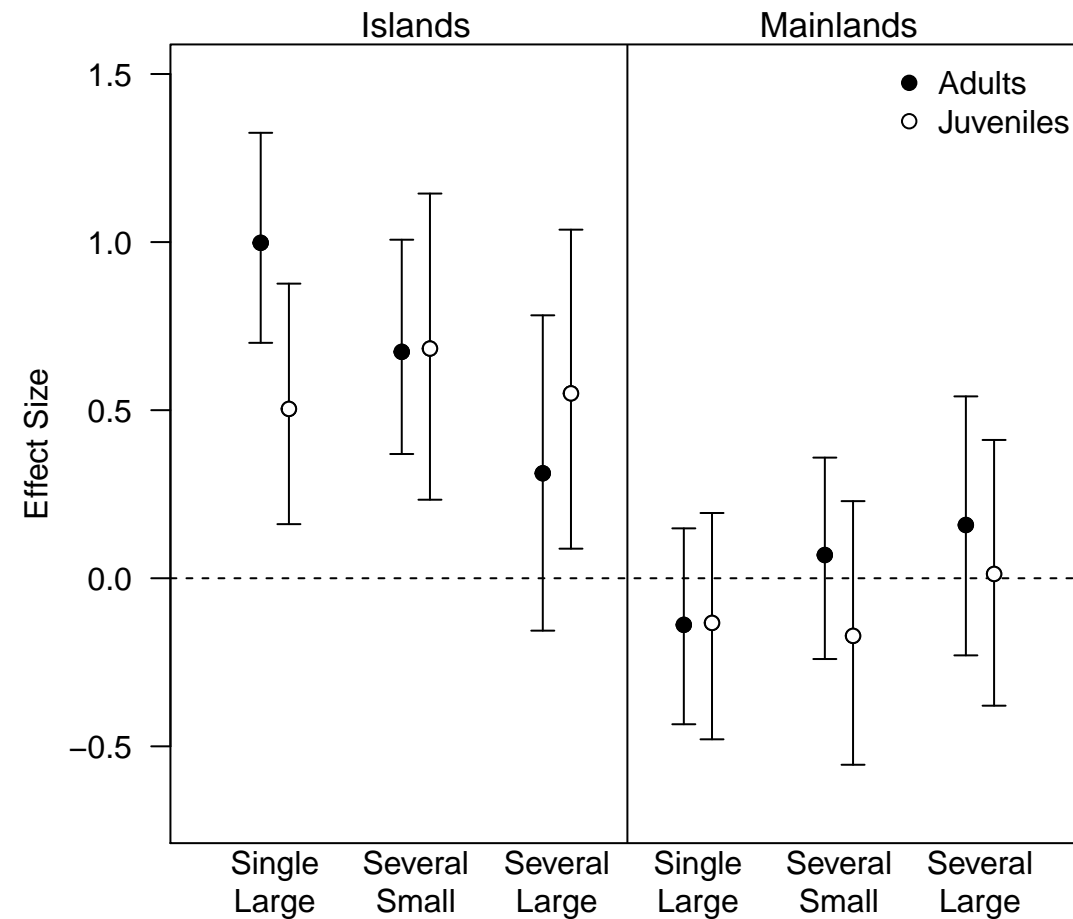
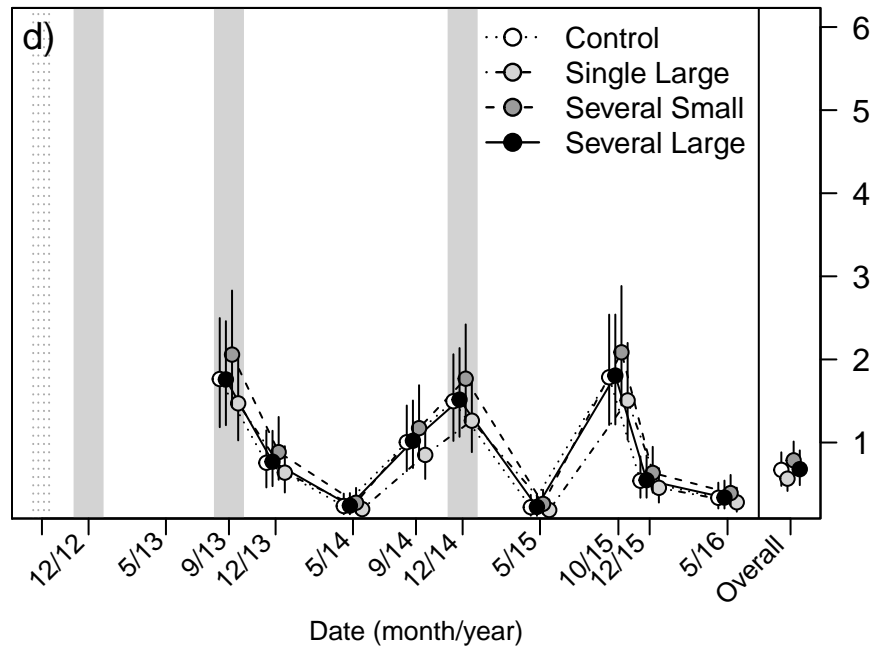
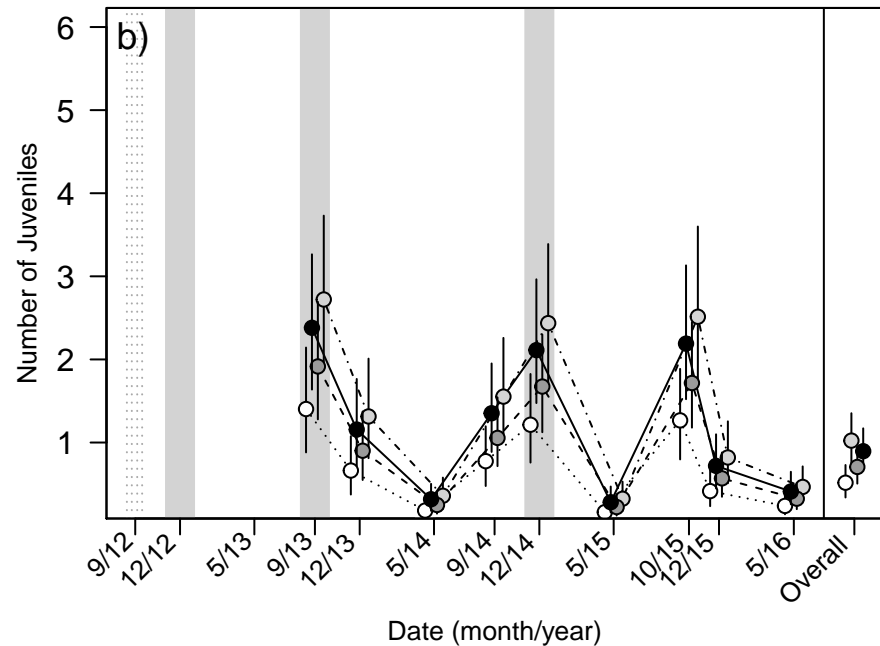
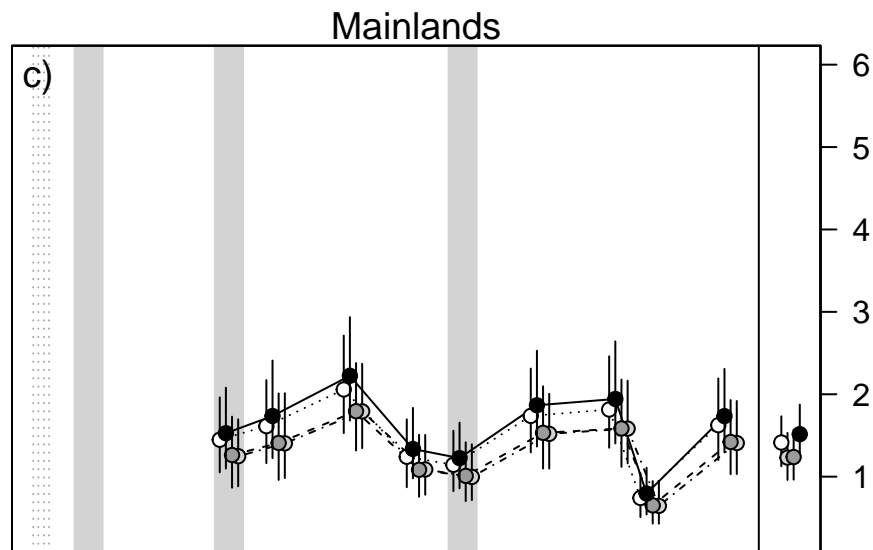
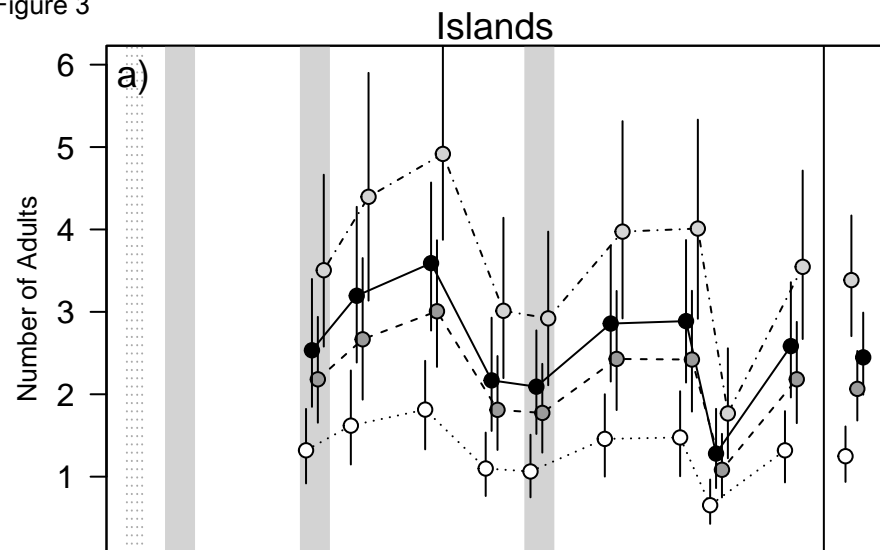


Figure 3



Supplementary Material for:

Title: Consumer responses to experimental pulsed subsidies in isolated vs. connected habitats.

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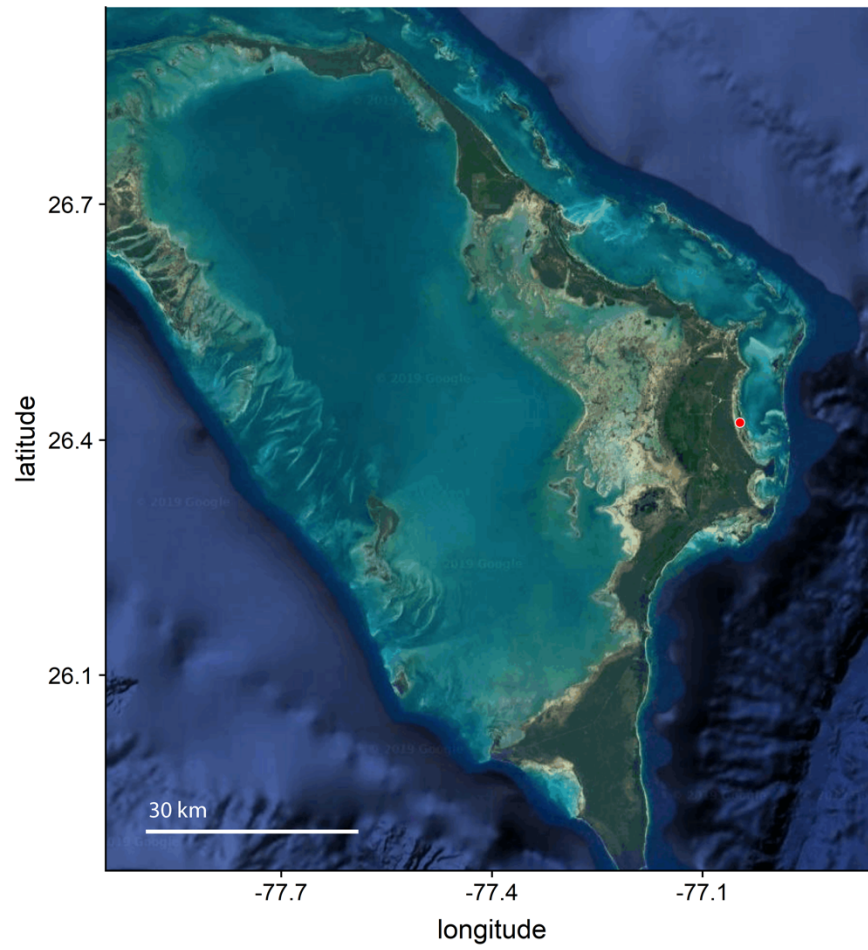


Figure S1A. Map of study site location off of Great Abaco, Bahamas shown in red.

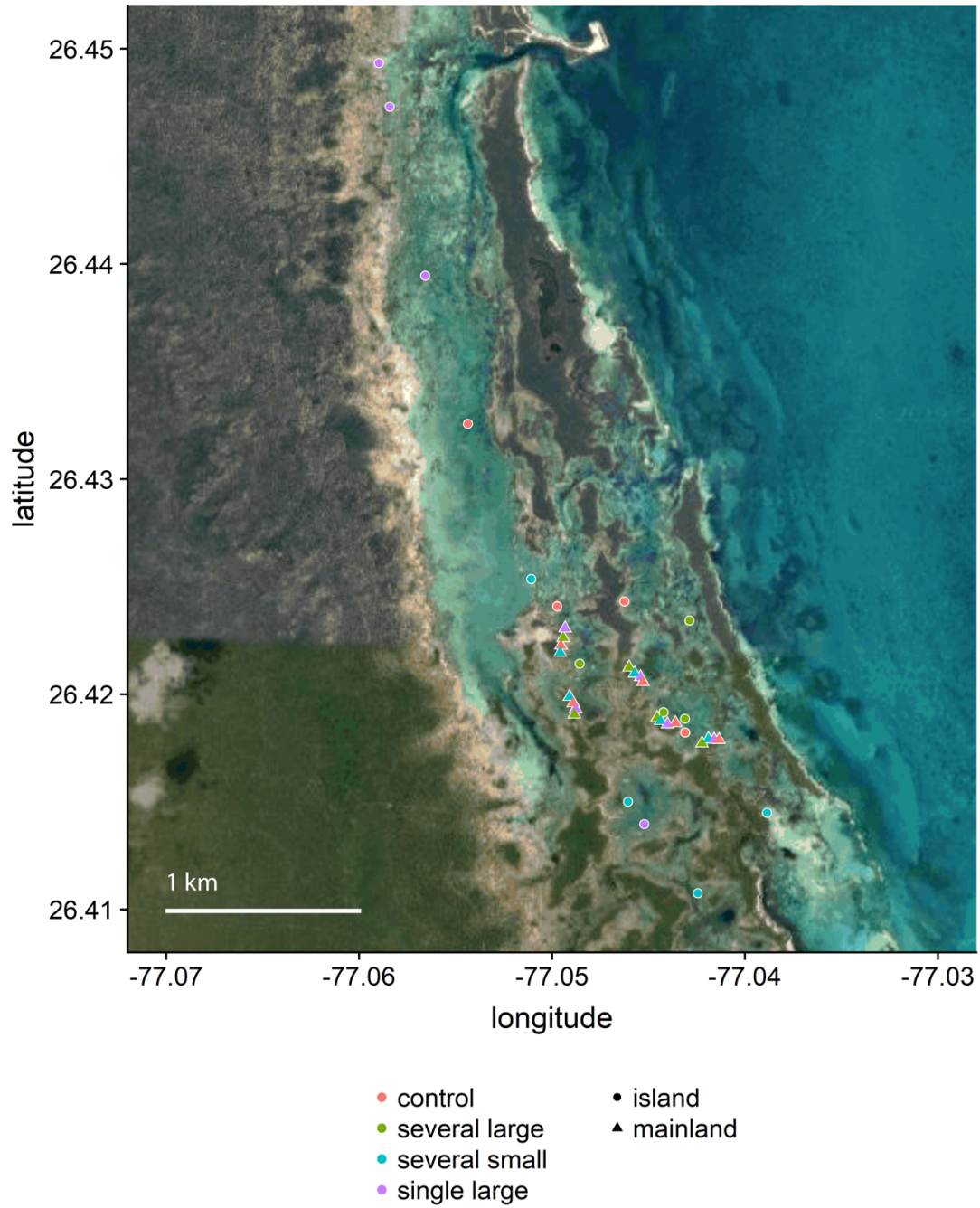


Figure S1B. Study site. Small islands are shown as circles, and mainland plots are shown as triangles.

Table S1. Lizard re-introductions to small islands

Experimental Unit	Seaweed Treatment	Date	Lizards reintroduced	Vegetated area (m ²)	Note
I-04	Control	May 2013	1 male	6.9	
E-B03	Several Large	May 2013	1 male	39.9	
S-01	Control	May 2013	1 male	44.0	
A-21	Single Large	September 2013	2 females + 1 male	4.3	Same as initial stocking
I-04	Control	May 2014	1 male	6.9	
R-03	Control	May 2014	1 male	13.7	

Natural seaweed deposition

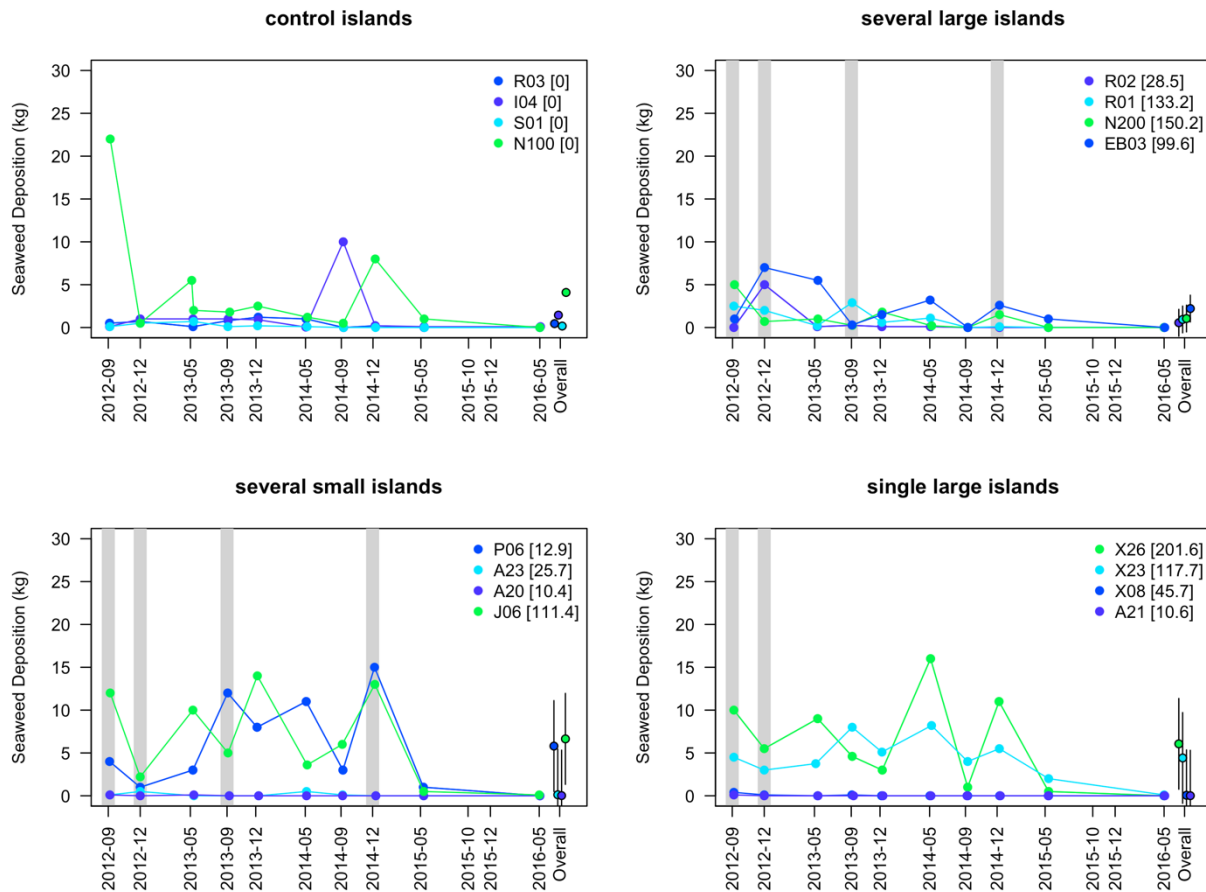


Figure S2. Natural seaweed deposition on small islands. Each panel shows a different seaweed treatment. The colors in the legend refer to the block (shared across panels), the labels are the experimental unit names (e.g. R03 is a small island), and the number in brackets following the unit name is the kg of seaweed added during each subsidy event for that experimental unit given its treatment and amount of vegetated area. The overall values are the mean \pm SD; mean values were used as a covariate in the diet and abundance models. The gray bars indicate when subsidies were applied for each treatment.

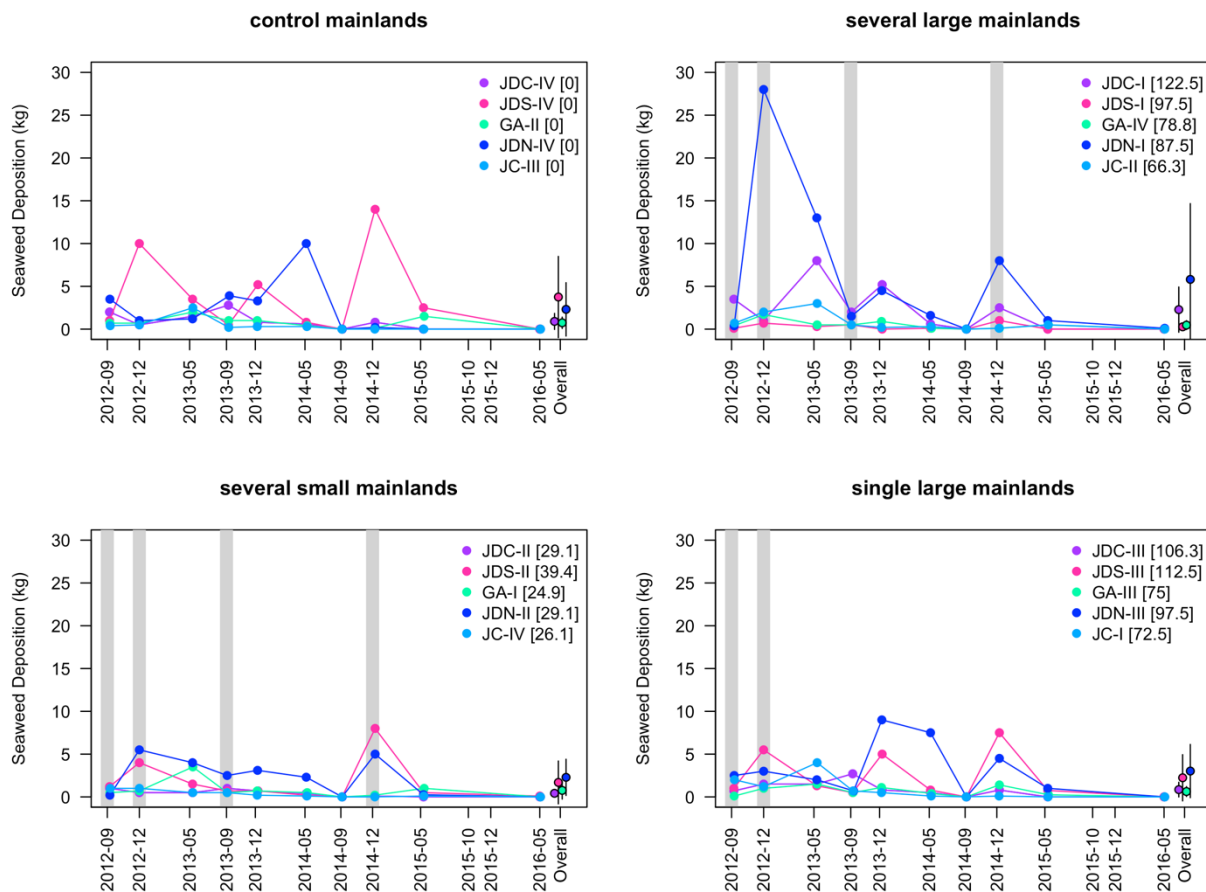


Figure S3. Natural seaweed deposition on mainlands. Each panel shows a different seaweed treatment. The colors in the legend refer to the block (shared across panels), the labels are the experimental unit names (e.g. JDC is a mainland, and each plot is numbered with Roman numerals), and the number in brackets following the unit name is the kg of seaweed added during each subsidy event for that experimental unit given its treatment and amount of vegetated area. The overall values are the mean \pm SD; mean values were used as a covariate in the diet and abundance models. The gray bars indicate when subsidies were applied for each treatment.

Effect of lipid extraction on lizard $\delta^{13}\text{C}$

To do a mathematical correction for lipid content, we need to establish a relationship between the C:N of the sample and the difference between the $\delta^{13}\text{C}_{\text{corrected}}$ and the $\delta^{13}\text{C}_{\text{uncorrected}}$, following Post et al. 2007 and Takimoto et al. 2008. For 10 lizard tissue samples collected during 2012 from small islands ($n = 3$), mainlands ($n = 3$), and the mainland source for small island lizards ($n = 4$), we split the tissue into two samples. For each lizard, on one sample we conducted lipid extraction and one sample was a control. The extraction procedure was as follows: extract for 15 minutes in 2:1 chloroform:methanol, followed by centrifugation at 200 rpm for 30 seconds. Lipid extraction had a small but significant effect on $\delta^{13}\text{C}$ ($p < 0.0001$), with extracted samples having higher $\delta^{13}\text{C}$. To adjust for this effect, we fit a linear regression with the difference between $\delta^{13}\text{C}_{\text{corrected}}$ and the $\delta^{13}\text{C}_{\text{uncorrected}}$ as the response, and the C:N ratio as the predictor (r^2 was 0.89, $p < 0.0001$). We corrected the $\delta^{13}\text{C}$ all of our lizard tissue samples using the C:N ratio of each sample and the fitted effects of the linear model.

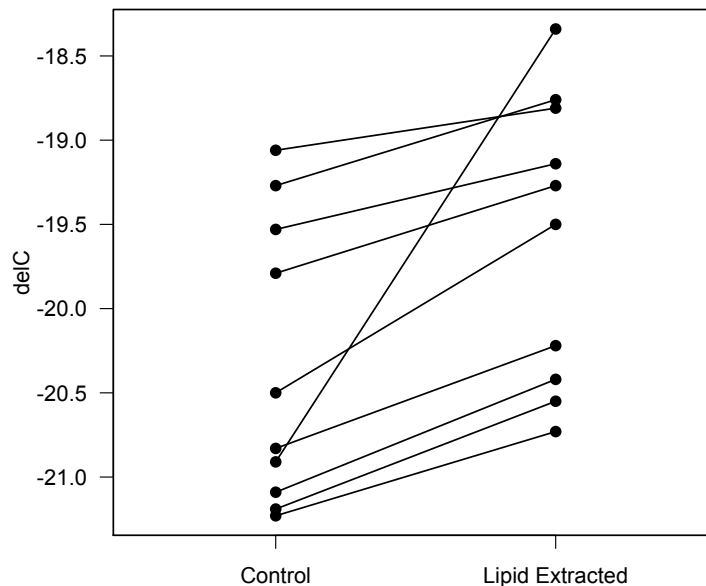


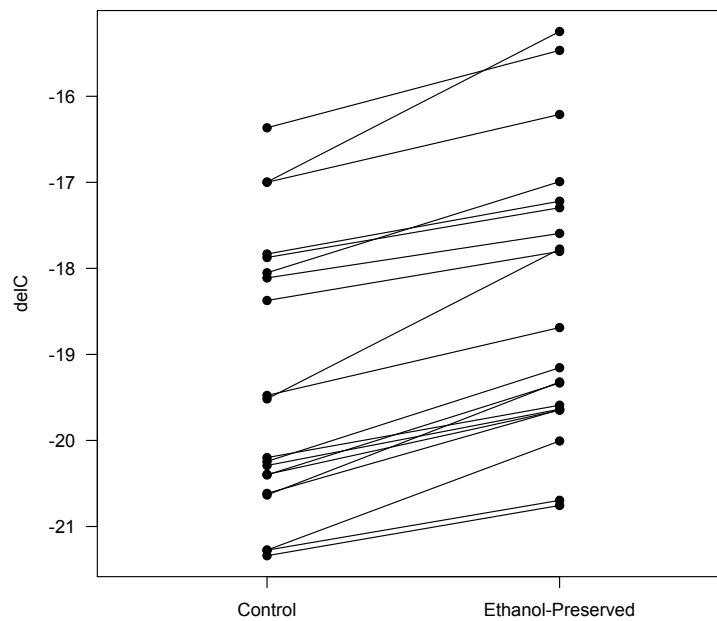
Figure S4

Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montana. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189.

Takimoto, G., D. A. Spiller, and D. M. Post. 2008. Ecosystem Size, but Not Disturbance, Determines Food-Chain Length on Islands of the Bahamas. *Ecology* 89:3001–3007.

Effect of ethanol preservation on lizard tail tissue $\delta^{13}\text{C}$

We collected tail tissue from 20 *Anolis sagrei* on Oahu, Hawaii (21.270004°, -157.815553°) in May 2016 to determine the effect of ethanol preservation on $\delta^{13}\text{C}$. We collected two tissue samples from each individual: one sample was kept refrigerated in the field and frozen without preservative within 2 hours of collection, and one sample was immediately preserved in 95% ethanol. All samples were dried at 55°C to constant mass prior to stable isotope analysis. To estimate the effect of ethanol preservation on $\delta^{13}\text{C}$, we fit a linear mixed model with $\delta^{13}\text{C}$ as the response, ethanol preservation as a fixed effect (yes vs. no), and a random effect for sample to account for the paired design. The conditional r^2 was 0.975, and the effect of preservation was statistically significant ($p < 0.0001$). The estimate of the ethanol effect from the model was that ethanol preservation increased $\delta^{13}\text{C}$ by 0.90955, and this value was used to correct the December 2012 pre-subsidy values for small island lizards used for visualization in Figure 1, Figure S8, and Figure S9.

**Figure S5**

Effect of acid fumigation on seaweed $\delta^{13}\text{C}$

We conducted acid fumigation to account for inorganic carbonates in the seaweed samples. Half of each sample served as a control, and half was acid fumigated following Harris et al. (2001). The acid fumigation procedure was as follows: 4 mg of each sample was placed into a silver capsule, the capsules were placed in a microplate wetted with 50 μL of pure water, the microplate was then placed in a glass desiccator with 3 mL of concentrated (12M) HCl for 24-96 hours. All samples were dried in a drying oven to constant mass prior to stable isotope analysis. To estimate the effect of acid fumigation on $\delta^{13}\text{C}$, we fit a linear mixed model with $\delta^{13}\text{C}$ as the response, acid fumigation as a fixed effect (yes vs. no), and a random effect for sample to account for the paired design. The conditional r^2 was 0.971, and the effect of acid fumigation was statistically significant ($p < 0.0001$). The estimate of the acid fumigation effect from the model was that acid fumigation decreased $\delta^{13}\text{C}$ by 0.7801. As a result, we used the stable isotope data from the acid fumigated samples in our mixing model.

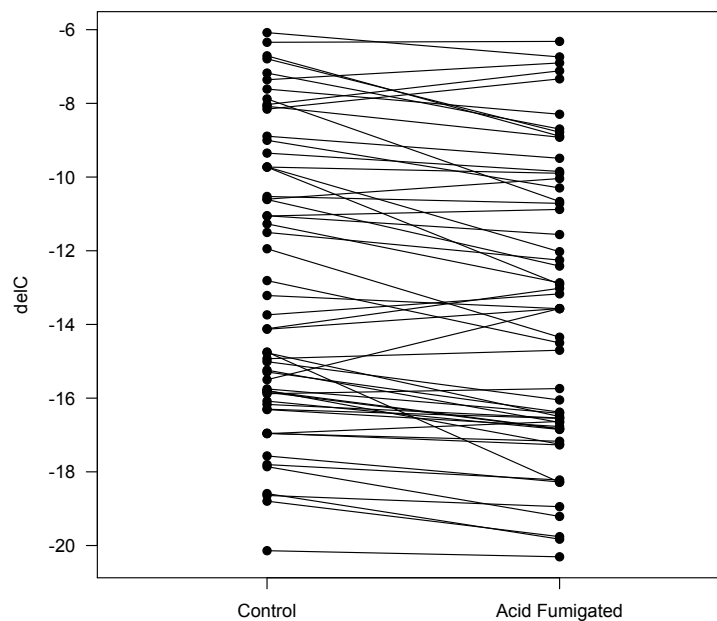


Figure S6

Harris, D., W. R. Horwath, and C. van Kessel. 2001. Acid fumigation of soils to remove carbonates prior to total organic carbon or CARBON-13 isotopic analysis. *Soil Science Society of America Journal* 65:1853.

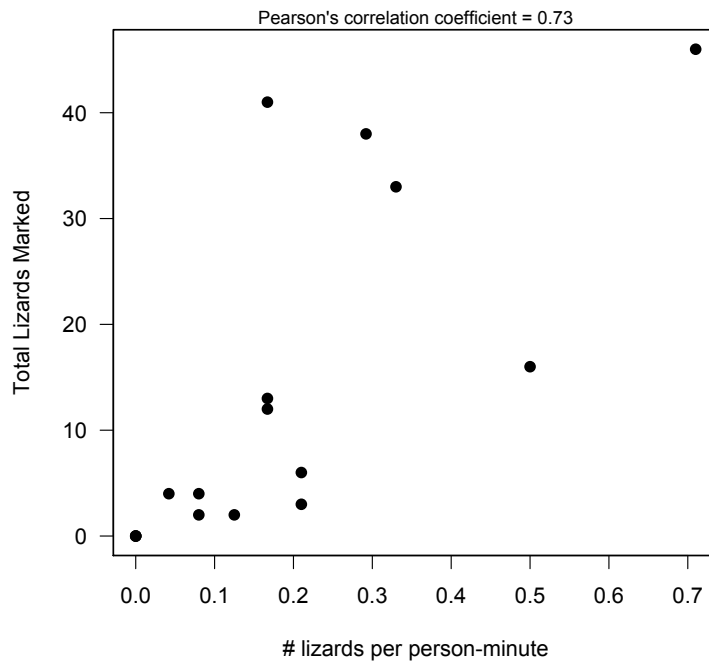


Figure S7. Correlation between lizard abundance index from timed surveys and the more extensive mark-resighting in October 2015.

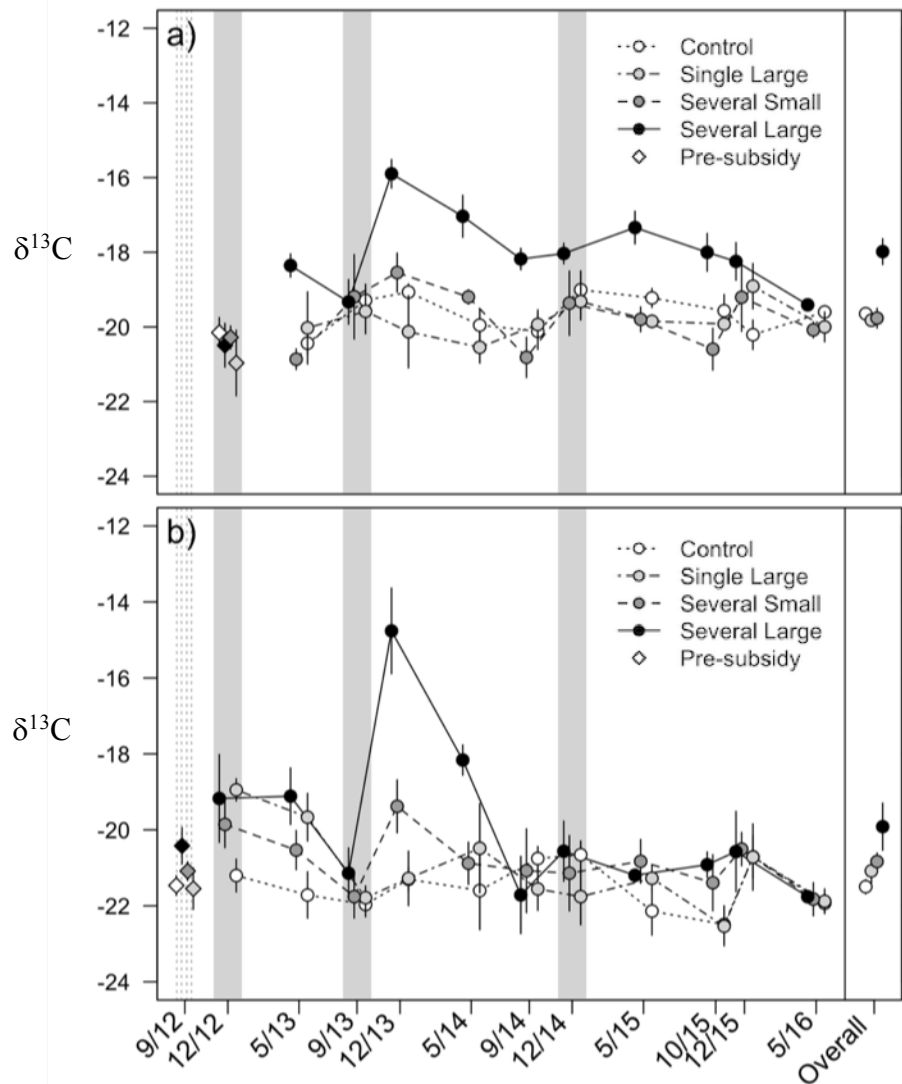


Figure S8. Raw $\delta^{13}\text{C}$ data for the lizard diet shift in response to subsidy. Individuals were averaged within each experimental unit by sampling period, and then treatment means were calculated across experimental unit means. The y-axis is mean $\delta^{13}\text{C}$ from stable isotope analysis of lizard tissue. The x-axis is the month/year of each sampling period. Gray shaded bars indicate when seaweed subsidies occurred. Points are jittered for visualization. The “single large” treatment was only applied during the first subsidy event, while the “several small” and “several large” treatments were applied during all three events. The combined magnitude of seaweed from all three “several small” applications was equal to the magnitude of a “single large” application. a) Diet shift in lizards on small islands over time. $\delta^{13}\text{C}$ values shown for island lizards on 12/12 are from the lizards used to colonize the islands initially. Lizards and seaweed were added to islands together on this date, thus the tissue samples from colonists on 12/12 reflect their diet prior to introduction on islands. b) Diet shift in lizards in plots on mainlands over time. The values on 9/12 are from resident lizards in mainland plots prior to subsidy.

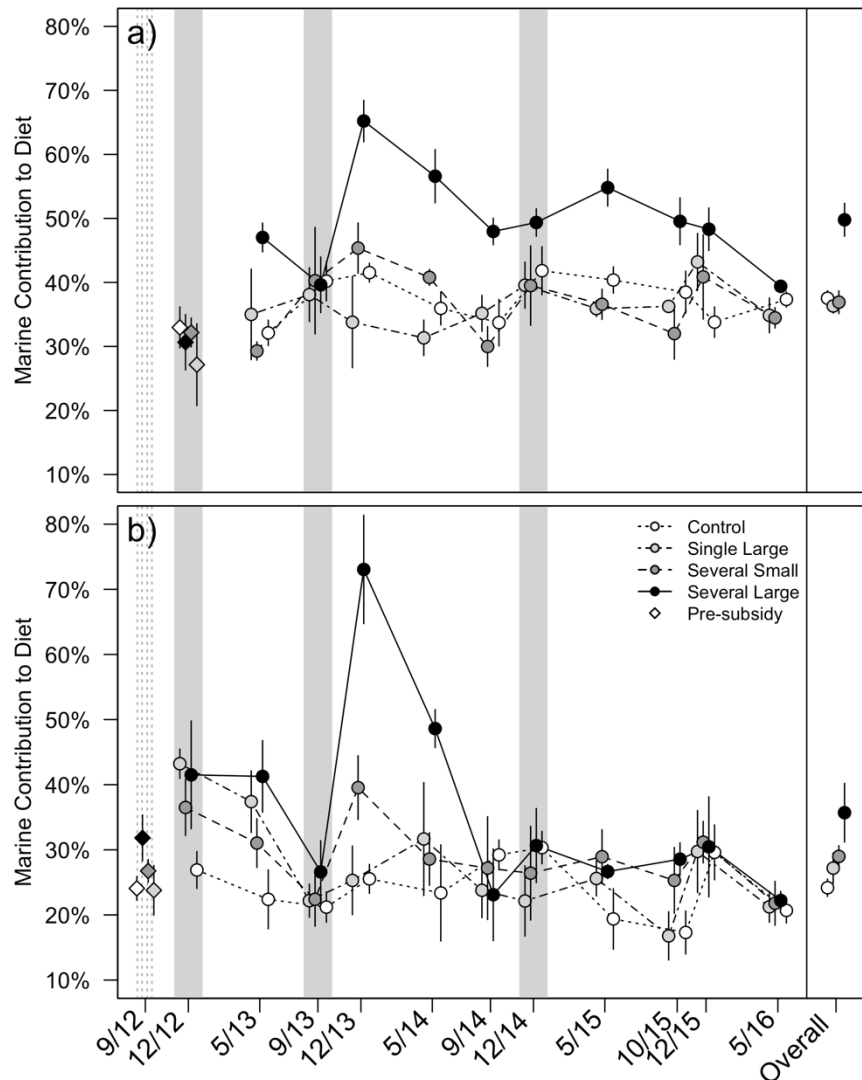


Figure S9. Raw percent marine contribution to lizard diets in response to subsidy. Means and SE were calculated from raw data output of percent marine from the stable isotope mixing model. Individuals were averaged within each experimental unit by sampling period, and then treatment means were calculated across experimental unit means. The y-axis is the percent of carbon in the diet contributed from marine sources (i.e., seaweed detritivores) estimated from $\delta^{13}\text{C}$ stable isotope analysis of lizard tissue. The x-axis is the month/year of each sampling period. Points are jittered for visualization. Gray shaded bars indicate when seaweed subsidies occurred. The “single large” treatment was only applied during the first subsidy event, while the “several small” and “several large” treatments were applied during all three events. The combined magnitude of seaweed from all three “several small” applications was equal to the magnitude of a “single large” application. a) Diet shift in lizards on small islands over time. Percent marine values shown for small island lizards on 12/12 are from the lizards used to colonize the islands initially. Lizards and seaweed were added to islands together on this date, thus the tissue samples from colonists on 12/12 reflect their diet prior to subsidy. b) Diet shift in lizards in plots on mainlands over time. The values on 9/12 are from resident lizards in mainland plots prior to subsidy.

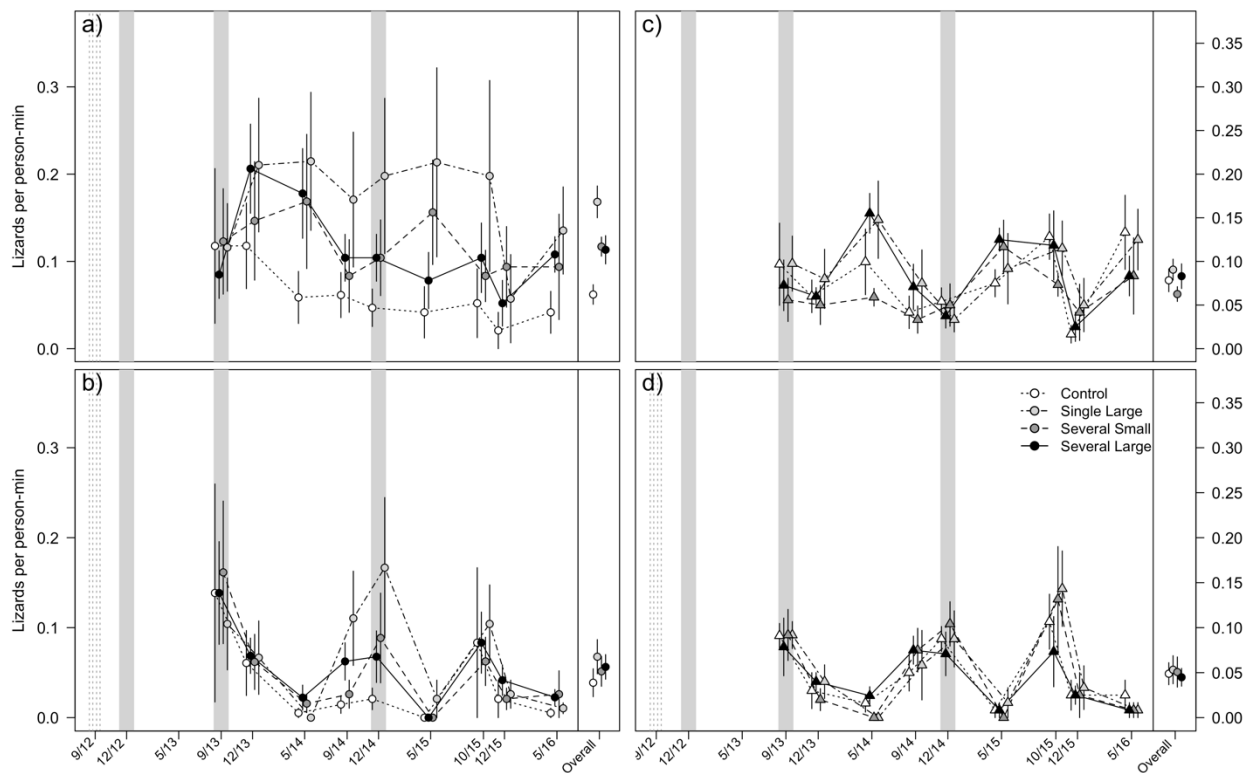


Figure S10. Raw data for lizard abundance index over time. The y-axis is mean number of lizards per person-minutes of search effort. If multiple censuses were performed on a unit during a sampling period their values were averaged, and then treatment means were calculated. Note that this representation does not have any corrections for varying effort among surveys. The x-axis is the month/year of each sampling period. Points are jittered for visualization. Gray shaded bars indicate when seaweed subsidies occurred. The “single large” treatment was only applied during the first subsidy event, while the “several small” and “several large” treatments were applied during all three events. The combined magnitude of seaweed from all three “several small” applications was equal to the magnitude of a “single large” application. Panels are a) small island adults, b) small island juveniles, c) mainland adults, d) mainland juveniles.

Precipitation Data

Climate data was downloaded from NOAA (<https://www7.ncdc.noaa.gov/CDO/cdo>). Observations begin in 1973 and extend to the present. The nearest locations to our study site with data were Nassau International Airport and Grand Bahama International Airport. Both stations are ~163 km from our study site, but the Nassau data has fewer missing observations during the study period and is shown here.

Spiller and Schoener (1995, 2008) used number of days with rain, rather than cumulative rainfall, as a measure of precipitation in the Bahamas. They argued that larger rain events lead to more fresh water running off the islands, and that number of days with rain is a better proxy for the availability of fresh water to organisms on the study islands.

The following plots show the number of rain days in each year at Nassau since 1977 (top, Fig. S11), and the number of rain days during intervals corresponding to our sampling periods from 2012-2016 (1) Jan-April, 2) May-September, 3) October-December (bottom, Fig. S11). The black line indicates the annual (top) and seasonal (bottom) means from 1977-2016, and the dashed line shows the start of the experiment at the end of 2012.

Spiller, D.A. and Schoener, T.W., 1995. Long-term variation in the effect of lizards on spider density is linked to rainfall. *Oecologia* 103:133-139.

Spiller, D.A. and Schoener, T.W., 2008. Climatic control of trophic interaction strength: the effect of lizards on spiders. *Oecologia* 154:763-771.

Figure S11 Annual Rain Days

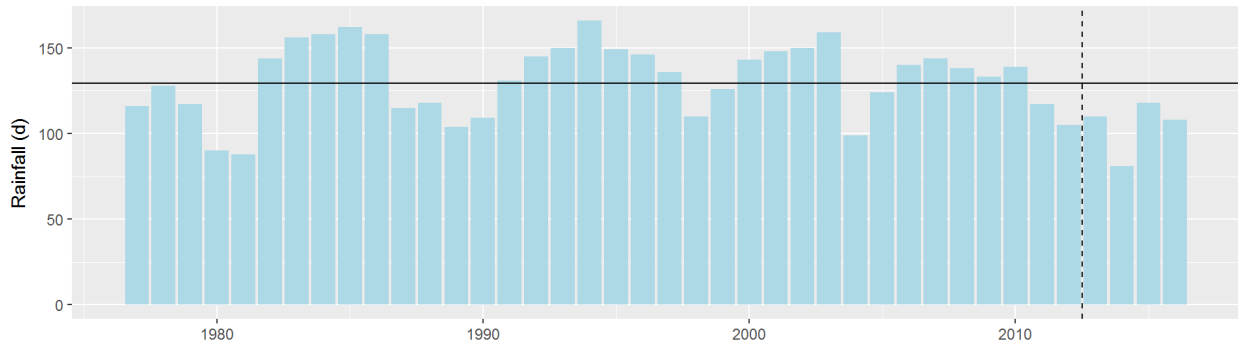


Figure S12 Seasonal Rain Days

