

# Marine subsidies have multiple effects on coastal food webs

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**Abstract.** The effect of resource subsidies on recipient food webs has received much recent attention. The purpose of this study was to measure the effects of significant seasonal seaweed deposition events, caused by hurricanes and other storms, on species inhabiting subtropical islands. The seaweed represents a pulsed resource subsidy that is consumed by amphipods and flies, which are eaten by lizards and predatory arthropods, which in turn consume terrestrial herbivores. Additionally, seaweed decomposes directly into the soil under plants. We added seaweed to six shoreline plots and removed seaweed from six other plots for three months; all plots were repeatedly monitored for 12 months after the initial manipulation. Lizard density (*Anolis sagrei*) responded rapidly, and the overall average was 63% higher in subsidized than in removal plots. Stable-isotope analysis revealed a shift in lizard diet composition toward more marine-based prey in subsidized plots. Leaf damage was 70% higher in subsidized than in removal plots after eight months, but subsequent damage was about the same in the two treatments. Foliage growth rate was 70% higher in subsidized plots after 12 months. Results of a complementary study on the relationship between natural variation in marine subsidies and island food web components were consistent with the experimental results. We suggest two causal pathways for the effects of marine subsidies on terrestrial plants: (1) the “fertilization effect” in which seaweed adds nutrients to plants, increasing their growth rate, and (2) the “predator diet shift effect” in which lizards shift from eating local prey (including terrestrial herbivores) to eating mostly marine detritivores.

**Key words:** *allochthonous inputs; Anolis sagrei; apparent competition; apparent mutualism; Conocarpus erectus; Exumas, central Bahamas; food webs; herbivory; lizards; marine subsidies; resource pulse; seaweed.*

## INTRODUCTION

Understanding the manner in which various factors influence species interactions in food webs is a central goal of current ecological research. A growing body of work has focused on the impact of allochthonous inputs (the flow of material and organisms across ecosystem boundaries) on recipient food webs (Polis et al. 1997, 2004, Huxel and McCann 1998, Marczak et al. 2007). Allochthonous inputs of nutrients for primary producers are ubiquitous (Polis et al. 2004), and their cascading effects on food web dynamics may be similar to those of in situ nutrients (Leroux and Loreau 2008). The effect of subsidized prey on local populations of predators and species in lower trophic levels has received much attention. Predators may switch from eating local prey to subsidized prey or eat both and become satiated, leading to an increase in local prey (“apparent mutualism”; Abrams and Matsuda 1996). This indirect positive effect of subsidized prey on local prey can last for a long

time if predator density is relatively unaffected by subsidized prey. However, a marked numerical response by predators may lead to a reduction in local prey (“apparent competition”; Holt 1977, Abrams et al. 1998), especially when the predators show a preference for local prey. Field experiments have shown that the indirect effect of subsidized prey on local prey can be positive (Nakano et al. 1999, Sabo and Power 2002a, Baxter et al. 2005, Birkhofer et al. 2007), negative (Polis and Hurd 1996a, Henschel et al. 2001, Murakami and Nakano 2002), or insignificant (Halaj and Wise 2002, Sabo and Power 2002b, Miyashita et al. 2003). In the case in which the indirect effect is negative and local prey are herbivores, subsidies can strengthen the top-down effects of predators on producers, thereby leading to an “apparent trophic cascade” (Polis et al. 1997). Conversely, a positive indirect effect can weaken the trophic cascade.

The specific effect of subsidized prey on local prey may depend on temporal scales of the processes operating in that system (Takimoto et al. 2002, Sears et al. 2004, Baxter et al. 2005). When subsidies occur in pulses, in the short term the indirect positive effect on

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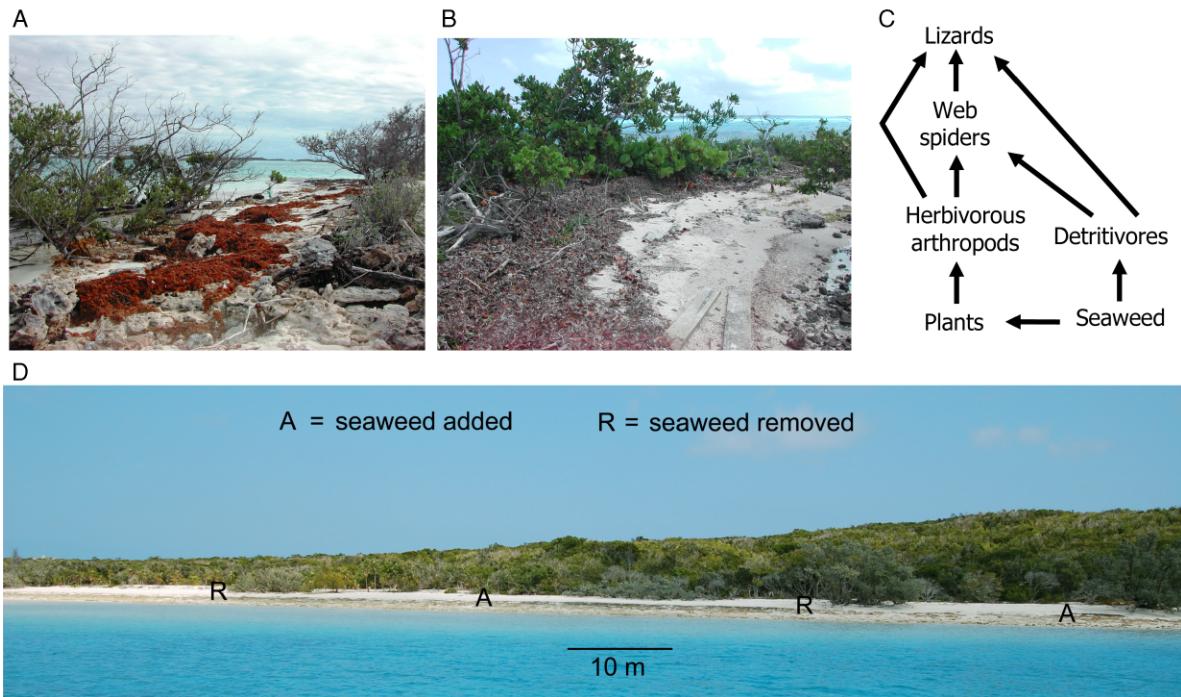


FIG. 1. Studies were conducted on shoreline habitats in the Exumas, a chain of islands located in the central Bahamas. (A, B) Photographs of seaweed on the shore of two islands in the fall following tropical storms. (C) Working model of the connections between marine resources and terrestrial food web components. (D) Photograph of an experimental island showing the approximate treatment locations.

local prey caused by predators switching and becoming satiated on subsidized prey may take precedence, whereas in the long term the negative effect caused by predators responding numerically to the subsidized prey may become predominant. For seasonal subsidy pulses, the overall effect can depend on the timescale of the subsidy pulse relative to the numerical response by predators (Takimoto et al. 2009).

Marine macrophytes (seaweed) deposited on shorelines support a rich array of primary and secondary consumers in many regions of the world (Polis and Hurd 1996b, Dugan et al. 2003, Stapp and Polis 2003, Barrett et al. 2005, Catenazzi and Donnelly 2007, Ince et al. 2007, Heck et al. 2008). In the Bahamas, large amounts of seaweed are deposited on shorelines in the fall following tropical storms and early cold fronts (Fig. 1A, B). We hypothesized that this seaweed represents a pulsed resource subsidy (sensu Sears et al. 2004, Yang et al. 2008) that is consumed by detritivores, which are eaten by terrestrial predators; those predators also consume terrestrial herbivores. Additionally, seaweed washed high onshore during storms may decompose directly into the soil and fertilize plants. Previously, we demonstrated that lizards reduce web spider populations (Schoener and Spiller 1996, Spiller and Schoener 1998) as well as amounts of herbivory on two different seashore shrubs, *Conocarpus erectus* and *Coccoloba uvifera* (Spiller and Schoener 1990, Schoener and Spiller 1999). Furthermore, we suggested

that lizards and spiders are subsidized by allochthonous detritivore prey (Spiller and Schoener 1996). A working model of the hypothesized connections between marine subsidies and the terrestrial food web subjects in this study may be found in Fig. 1C.

To investigate the impact of seasonal marine subsidies on the terrestrial food web, we manipulated amounts of seaweed on shoreline plots during the fall and monitored the food web subjects for a full year. We hypothesized that addition of marine subsidies would enhance terrestrial herbivory in the short term (fall and winter) when the predators switch from eating herbivores to marine detritivores. In the long term (spring and summer), we hypothesized that predators would respond numerically to marine subsidies and then switch back to eating mostly herbivores as the detritivores declined, leading to an “apparent trophic cascade” (sensu Polis et al. 1997) in which subsidies strengthen the positive effect of predators on plants. In short, we predicted that addition of marine subsidies would increase herbivory in the short term and decrease herbivory in the long term. Although other groundbreaking field experiments have examined the impact of subsidized prey on food webs, to our knowledge no previous experiment had run for more than five months. Hence, the present experiment is the first designed to measure and distinguish the short- and long-term effects of pulsed resource subsidies. Additionally, to link the experimental results to phenomena

occurring naturally in the system, we conducted a complementary survey of the relationships between natural variability in amounts of marine subsidies and characteristics of island food webs.

## METHODS

### *Natural history of the study system*

Studies were conducted on shoreline habitats in the Exumas, a chain of islands located in the central Bahamas. Vegetation consisted largely of perennial shrubs and trees. We focused on one of the commonest species, *Conocarpus erectus* (buttonwood), as in previous studies (Schoener and Spiller 1999, Spiller and Schoener 2007). Confirmed identifications of buttonwood herbivores are Coleoptera (Chrysomelidae, *Chaetocnema brunnescens*, *Metachroma felis*, *Cryocephalus* sp.; Curculionidae, *Artipus floridanus*; Elateridae, *Conoderus* sp.) and Lepidoptera (Noctuidae, *Collomena filifera*; Psychidae, *Biopsyche* sp.; Gelechiidae, unidentified species); leafhoppers (Hemiptera) are occasionally observed on foliage. *Anolis sagrei*, the brown tree lizard, is the most abundant vertebrate predator (see Plate 1). Other conspicuous predators are the common web spiders *Metepeira datona*, *Eustala cazieri*, and *Argiope argentata*; other rarer species are listed in Spiller and Schoener (1998).

Seaweed deposited on shorelines (wrack) consists mostly of the brown algae *Sargassum*, including pelagic (*S. fluitans*, *S. natans*) as well as benthic species (probably *S. hystrix*, *S. polyceratium*); sea grasses (*Thalassia testudinum*, *Syringodium fuliforme*) are also common on some shorelines. The predominant seaweed consumers, particularly in terms of biomass, are amphipods (*Tethorchestia* spp.), followed by several unidentified dipterans. We have observed lizards climbing down from trees to forage for amphipods and dipterans in nearby clumps of seaweed and have frequently seen them foraging in the intertidal. We have also observed aggregations of web spiders (*M. datona*) catching dipterans in areas with large amounts of seaweed. Seaweed deposition appears to be seasonal, occurring mostly in the fall; this pattern may be driven by high winds associated with tropical storms and early cold fronts combined with the phenology of the seaweed species. The most extreme deposition events we have observed were in the fall following hurricanes, which have become more frequent in the Atlantic Basin during the past decade (Elsner et al. 2008). An extreme seaweed deposition event in North Carolina, USA, associated with a hurricane is described by Blomquist and Pyron (1943).

### *Experimental manipulation of seaweed*

To test the effect of a seasonal pulse of marine subsidies on the terrestrial food web, we manipulated amounts of seaweed on shoreline plots located on three relatively large (area > 10<sup>4</sup> m<sup>2</sup>) islands. In May 2006 we staked out four 10 × 10 m plots on the shoreline of each island; plots began at approximately the high tide level and were separated by a 10–30-m buffer area to reduce

contamination between treatments (e.g., movements of consumers from one plot to another). We used a systematically interspersed design (Hurlbert 1984) in which the end plot along the shore on each island was randomly assigned to a treatment (seaweed added, seaweed removed) by tossing a coin, and treatments were assigned to the remaining plots in an alternating manner (Fig. 1D). Seaweed was manipulated in three sessions during fall 2006 (September, November, and December), coinciding with the period when high seaweed deposition events occur naturally. Amount of seaweed added each session to each subsidized plot was ~2.5 kg/m<sup>2</sup>, which is within the range observed naturally deposited on shorelines (Appendix C). The locations of the study plots were not close to tidal creeks or other types of water currents that could have transported local nutrients away from subsidized plots. The study islands were ideal for this experiment because normal tidal fluctuations (1.0–1.5 m) were minimal. Rainwater runoff was low because the islands are mostly flat (elevation < 5 m) and composed of porous limestone. We found no evidence that the seaweed added to subsidized plots was transported to adjacent removal plots. Food web subjects depicted in Fig. 1C were monitored for a full year as follows.

Marine detritivore abundance was sampled with bowls (~0.5 L) filled with water and a trace amount of detergent. In each plot, four bowls were placed in a row parallel to the shore in the center of the plot. After 24 h, all specimens were collected and preserved in the field and transported to the University of California, Davis, where they were examined under a dissecting microscope and identified to order (or lower when possible) and measured with an ocular micrometer. Biomass of amphipods was estimated using a mass-length regression equation derived by measuring the length of 20 different-sized amphipods that were then dried and weighed (Appendix A); biomasses of other arthropods (some were not detritivores) were estimated using published taxon-specific length-mass power equations (Appendix A). Detritivores were sampled once before seaweed manipulations and six times after (dates are shown in Fig. 2A).

Lizards (*A. sagrei*) were the major predator subjects, as in our previous studies. To measure their abundance, we attempted to capture and individually mark all lizards in each plot during four sessions (dates in Fig. 2B). During each session, 1–4 persons worked for 3–5 consecutive days on each island, spending approximately the same amount of time in each plot; approximately 12 person-hours were spent in each plot on each island. Lizards were captured either by hand or with a noose, and all were marked with a spot of paint on their backs. Because a few lizards in each plot were too difficult to catch, we recorded the numbers of unmarked lizards observed the last day (<10% of the lizards observed on that day were unmarked); the sum of the number of unmarked lizards observed on the last day and the number of lizards marked in that plot during the entire

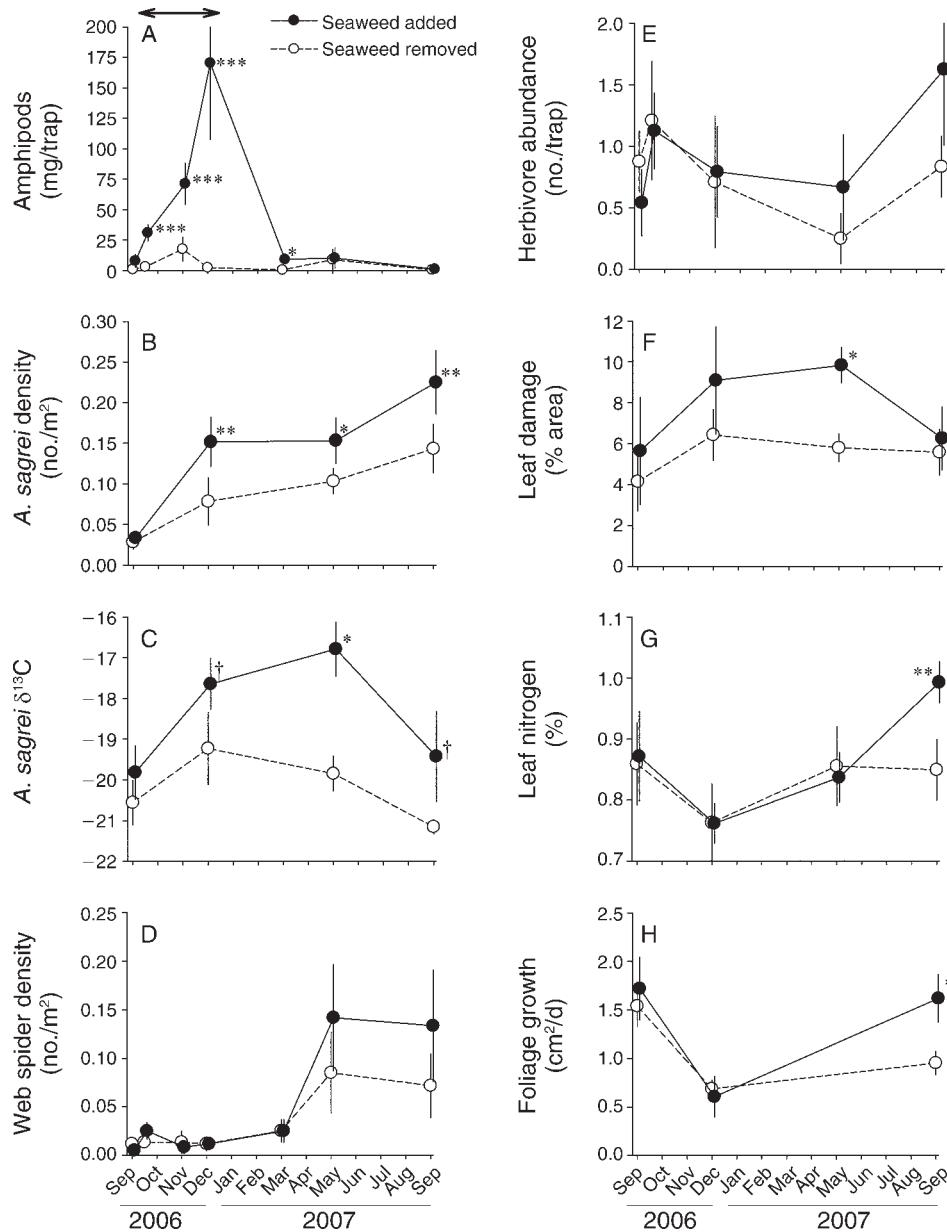


FIG. 2. Effect of seaweed manipulations on the measured food web components (mean ± SE): (A) biomass of amphipods in ground bowl traps (double-ended arrow denotes the manipulation period); (B) lizard (*Anolis sagrei*) density; (C) lizard stable-isotope content; (D) web spider density; (E) relative abundance of herbivorous arthropods in aerial sticky traps; (F) percentage of leaf area damaged; (G) leaf nitrogen content; and (H) foliage growth. The first measurements, taken in September 2006, are the pre-manipulation values. Symbols are the means of the values in plots with seaweed added and removed. Repeated-measures MANOVA (post-manipulation dates) for overall treatment effect and time × treatment effect, respectively, are: (A)  $F_{1,8} = 50.1$ ,  $P < 0.0001$ ;  $F_{5,4} = 5.1$ ,  $P = 0.069$ ; (B)  $F_{1,8} = 16.6$ ,  $P = 0.002$ ;  $F_{2,7} = 2.8$ ,  $P = 0.129$ ; (C)  $F_{1,5} = 10.1$ ,  $P = 0.012$ ;  $F_{2,4} = 15.8$ ,  $P = 0.013$ ; (D)  $F_{1,8} = 1.1$ ,  $P = 0.33$ ;  $F_{4,5} = 2.8$ ,  $P = 0.82$ ; (E)  $F_{1,7} = 10.0$ ,  $P = 0.016$ ;  $F_{2,6} = 0.03$ ,  $P = 0.97$ ; (F)  $F_{1,7} = 8.9$ ,  $P = 0.021$ ;  $F_{2,6} = 3.0$ ,  $P = 0.127$ ; (G)  $F_{1,8} = 0.86$ ,  $P = 0.38$ ;  $F_{2,7} = 5.0$ ,  $P = 0.044$ ; (H)  $F_{1,8} = 0.32$ ,  $P = 0.59$ ;  $F_{1,8} = 4.4$ ,  $P = 0.068$ . Within-date ANOVA treatment effects (step-down Bonferroni-adjusted) are denoted as: †  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

session was used as the total abundance. We are confident that nearly all the lizards present in each plot were counted. To assess for movements of lizards between plots, during the first two sessions most of the captured lizards were also permanently tagged with a unique color pattern of elastomeric material (Northwest

Marine Technologies, Shaw Island, Washington, USA) injected subdermally in the upper portions of their limbs. Lizards captured during subsequent sessions were carefully inspected for subdermal tags.

To test the effect of seaweed manipulations on lizard diets, we performed stable-isotope analysis on the tail



PLATE 1. The tree lizard, *Anolis sagrei*, foraging on the rocky shoreline with seaweed in the foreground. Photo credit: D. Spiller.

tips (~2 cm) from three adult (or nearly adult) lizards captured in each plot during each session on two of the three experimental islands. The third experimental island was omitted from the analysis because it did not have at least three lizards in each plot during the first half of the experiment. Lizards were more abundant on all islands during the second half of the experiment, and analysis of all three islands during this period may be found in Appendix B. Marine producers are relatively more enriched in  $^{13}\text{C}$  than terrestrial  $\text{C}_3$  plants (Peterson and Fry 1987), and this enrichment is transferred to the tissue of their consumers ( $\text{C}_4$  plants were rare in our study sites). Stable-isotope ratios are measured in “delta” units, expressing a relative deviation from standard values (Post 2002). Increased  $\delta^{13}\text{C}$  was used to measure the shift from terrestrial-based to marine-based prey (as in Anderson and Polis 1998). To measure variation among plots in terrestrial and marine baselines, we analyzed samples of leaves taken from the six largest plants present and seaweed in each plot during each session. Sample preparation and analysis details are in Appendix B.

Web spiders were censused by carefully searching the vegetation and ground in each plot and recording the number of spiders or fresh webs observed. Census dates are in Fig. 2D.

Relative abundance of herbivorous arthropods was measured with aerial sticky traps ( $22 \times 14$  cm sheets of clear plastic coated with Tangletrap adhesive [Tanglefoot, Grand Rapids, Michigan, USA] on one side). In each plot, four traps were tied to *C. erectus* branches ~1 m above the ground. Traps were taken down after 24 h, and the captured arthropods were identified to order or

lower. We assumed that Coleoptera, Lepidoptera, and Hemiptera (Sternorrhyncha and Auchenorrhyncha) were herbivores; most Coleoptera were Chrysomelidae (predatory taxa, e.g., Coccinellidae, were rare). Sampling dates may be found in Fig. 2E.

Leaf damage and foliage growth rate were measured on two *C. erectus* plants in each plot (except for two plots that had only one) during three different time intervals: May–September 2006 (before seaweed manipulations), September–December 2006, and May–September 2007. At the beginning of each time interval, on each plant four randomly chosen branches with apical meristems were tagged and the most distal leaves present were marked with ink. At the end of each time interval, only leaves that emerged after the beginning (those more distal than the marked ones) were collected. The total number of new leaves from each plant were counted, and 20 randomly chosen leaves were immediately pressed and then photographed. Total leaf and damaged areas were measured digitally from photographs using SigmaScan Pro Image Analysis System (SPSS Science, Chicago, Illinois, USA). Percentage of leaf area damaged on each plant was computed by summing the damaged areas of all leaves photographed and dividing by the sum of the total leaf areas. Foliage growth rate was the number of leaves collected multiplied by the mean leaf area from each plant divided by the number of days elapsed from branch marking to leaf collecting. An attempt to measure leaf damage and growth using this method from December 2006 to May 2007 (the dry season) was unsuccessful because no growth occurred on most of the tagged branches. Therefore, leaf damage was measured in May 2007 on five randomly chosen leaves

from four branches on each plant (20 leaves per plant). Leaf nitrogen content for each plant was measured with the mass spectrometer used for isotope analysis (Appendix B).

For each response variable, mean values for each plot on each post-manipulation date were analyzed using repeated-measures MANOVA with block (island) and treatment (seaweed added, removed) as the main (between-subjects) factors and time (sampling date) as the repeated (within-subject) factor. We used rmMANOVA because it contains fewer assumptions (e.g., sphericity) than does rmANOVA. For hypothesis testing, the treatment effect was one-tailed for lizard abundance, foliage growth, and leaf nitrogen, because we predicted that seaweed addition would increase these variables; two-tailed tests were used for the other variables. To test each hypothesis, the  $P$  value for the overall treatment effect was used when the time  $\times$  treatment interaction  $P$  value was  $>0.10$ . When the interaction  $P$  value was  $<0.10$ , treatment effects from separate ANOVAs on each sampling date were used; significance levels were then adjusted for multiple comparisons using the step-down Bonferroni method (SAS Institute 1999). For descriptive purposes, adjusted  $P$  values are given for all variables on all dates in the figures. To account for initial variation among plots, the initial (pre-manipulation) measurements were used as a covariate in the rmMANOVA of the post-manipulation measurements. If the covariate was significant ( $P < 0.05$ ), it was included in the model, otherwise it was dropped; the covariate was significant only in the herbivore abundance and leaf damage analyses. Distributions of marine detritivore, lizard, spider, and herbivore abundances and foliage growth rates within dates appeared to be approximately lognormal, and the standard deviations of the plots within treatments tended to be proportional to the means; therefore, the data were log-transformed to normalize the distributions and equalize the variances (Neter et al. 1996). Percentage of leaf damaged and leaf nitrogen content were arcsine square-root transformed, which yielded approximately equal variances. Data presented in figures are untransformed.

#### *Natural variation in marine subsidies and food web components*

In May 2007 we staked out 29  $10 \times 5$  m plots on the shoreline of three large islands. All plots were oriented on the windward (east) side of the island and contained at least two buttonwood plants, along with other shrubs. Plots began at approximately the high-tide level with the long axes parallel to the shoreline and were separated by at least 30 m. Seaweed biomass present on each plot was visually estimated in September, November, and December 2007. To calibrate our estimates, we visually estimated seaweed present in 21 areas outside the study plots and then collected and weighed the seaweed; visual estimates were highly correlated with measured amounts ( $r = 0.96$ ,  $P < 0.001$ ; Appendix C). We hoped to obtain

an even distribution of seaweed biomasses on the plots that would be appropriate for correlation analyses. However, more than half of the plots received little or no seaweed during the study period. Therefore, plots were divided into two categories: high subsidies ( $>1$  kg mean biomass of seaweed present averaged over the three censuses;  $n = 11$ ) and low subsidies ( $\leq 1$  kg;  $n = 18$ ). Data on food web components were taken in September and December 2007 following the procedures described earlier in *Experimental manipulation of seaweed*. For each variable, an ANOVA was performed on the mean value for each plot in the high- vs. low-subsidy groups. To account for variation among plots in vegetation structure, maximum vegetation height was measured within a 25-cm radius of 27 uniformly spaced points within each plot. Mean vegetation heights were similar in high-subsidy ( $122 \pm 21$  cm [mean  $\pm$  SE]) and low-subsidy ( $135 \pm 15$  cm) plots ( $F_{1,27} = 0.25$ ,  $P = 0.62$ ). Mean vegetation height was positively correlated with lizard abundance ( $r = 0.48$ ,  $P = 0.008$ ), as expected, and therefore was included as a covariate in the analysis of lizards. Variables were transformed for analyses as described earlier in *Experimental manipulation of seaweed*.

## RESULTS

### *Experimental manipulation of seaweed*

Seaweed manipulation during fall 2006 caused a marked increase in marine detritivores in the subsidized plots. Biomass of amphipods (the major detritivores) in December 2006 was 79 times higher in plots with seaweed added than in plots with seaweed removed (Fig. 2A). After the manipulations, amphipods declined in subsidized plots and the difference between treatments diminished. Overall mean amphipod biomass was nine times higher in subsidized plots than in removals. Biomasses of other arthropod taxa collected in bowl traps were also higher in subsidized than in removal plots during fall 2006, and some remained higher during winter and spring 2007, well after the manipulations (Appendix A).

Numbers of lizards (*A. sagrei*) increased in both treatments during the experiment, but more so in subsidized plots (Fig. 2B). After three months of seaweed manipulations (December 2006) the mean number was 93% higher in subsidized plots than in removals. Following the manipulations (May and September 2007), the difference between treatments declined slightly. The overall mean of the three post-manipulation censuses was 63% higher in subsidized plots. During the September 2006 and December 2006 capture sessions, 280 lizards were individually marked with subdermal tags; 65 of these tagged lizards were recaptured during subsequent sessions, and all were found in the same plot where they were originally captured.

Stable-isotope analysis revealed that lizard  $\delta^{13}\text{C}$  values became higher in subsidized plots than in removals (Fig. 2C), indicative of a shift in lizard diet

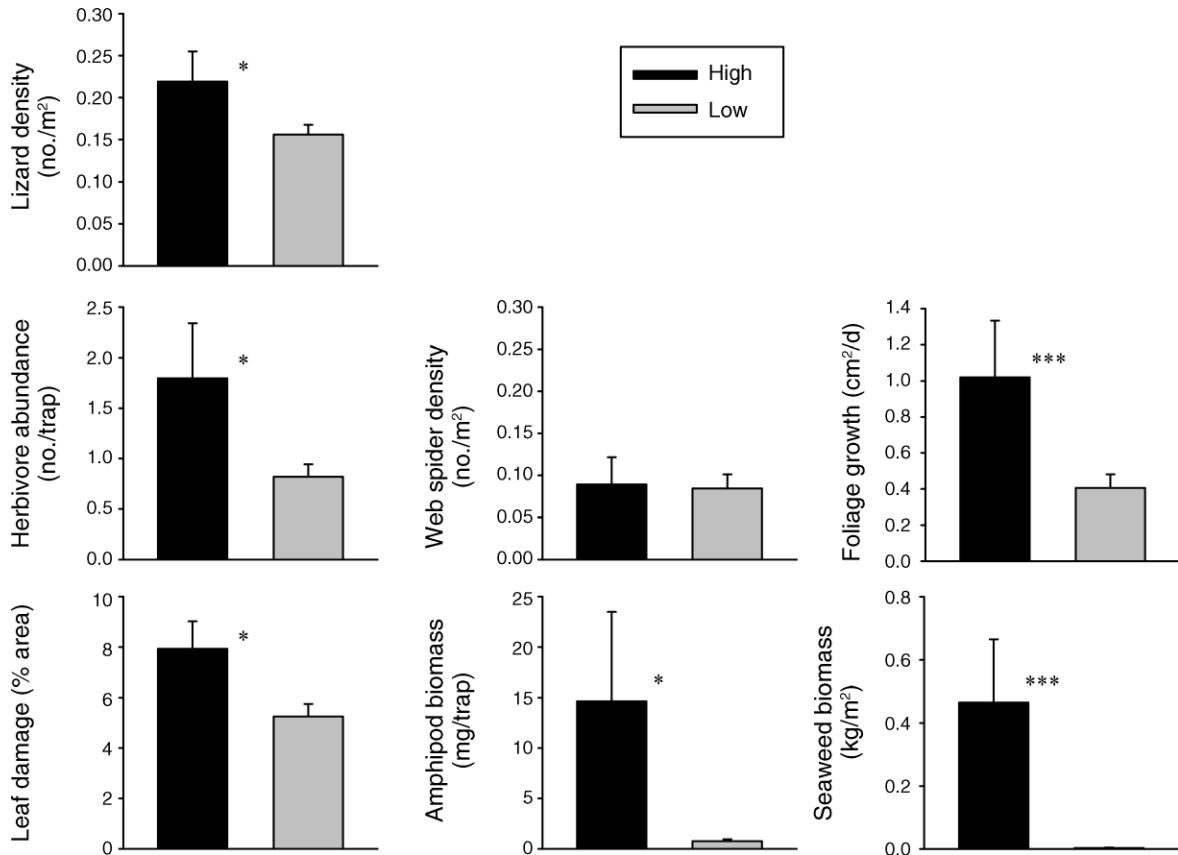


FIG. 3. Comparisons of food web variables (mean + SE) between plots with naturally high ( $n = 11$ ) and low ( $n = 18$ ) seaweed deposition. For high vs. low comparisons: \*  $P < 0.05$ ; \*\*\*  $P < 0.001$ .

composition toward more marine-based prey. Values in subsidized plots peaked in May 2007, when the difference between treatments was greatest, and declined in September 2007. Results of an isotope mixing model incorporating isotopic signatures for marine and terrestrial baseline resources show the same pattern (Appendix B).

Numbers of web spiders were nearly identical in the two treatments during the first six months of the experiment (Fig. 2D). In May and September 2007, they tended to be higher in subsidized plots, but no differences were significant.

Numbers of herbivorous arthropods caught in aerial sticky traps were similar in subsidized and removal plots during the first three months of the experiment (Fig. 2E). In May and September 2007 herbivore numbers tended to be higher in subsidized plots. Although no date-specific comparison was significant, the overall treatment effect in repeated-measures MANOVA was significant ( $F_{1,7} = 10.0$ ,  $P = 0.016$ ).

Leaf damage was higher in subsidized plots than in removals, particularly in May 2007 when damage was 70% higher (Fig. 2F). In September 2007, damage in subsidized plots declined and was similar to that in removals.

Leaf nitrogen percentages were nearly identical in the two treatments during the experiment until September 2007 when they became significantly higher in subsidized plots (Fig. 2G). Similarly, foliage growth rate was nearly identical in the two treatments at the beginning of the experiment and became significantly higher in subsidized plots at the end (Fig. 2H).

#### Natural variation in marine subsidies and food web components

Seaweed estimates recorded in September, November, and December 2007 on the 29  $10 \times 5$  m plots varied from 0 to 6.5 kg/m<sup>2</sup> (Appendix C); all plots designated to the high-subsidy category had consistently more seaweed than those designated to the low-subsidy category. Mean seaweed biomass was 159 times greater in high-subsidy plots than in low-subsidy plots (Fig. 3). Amphipod biomass was 19 times greater in high-subsidy plots than in low-subsidy plots. Web spider abundances were nearly identical in plots with high and low subsidies. All other variables were significantly higher in high-subsidy plots than in low-subsidy plots: number of lizards was 40% higher, number of herbivorous arthropods caught in sticky traps was 119% higher, leaf

damage was 51% higher, and foliage growth was 152% higher.

#### DISCUSSION

Seaweed manipulations had multiple effects in the terrestrial food web. Lizards, herbivorous arthropods, leaf damage, and foliage growth became significantly higher in subsidized plots than in removal plots. We suggest two causal pathways for the effects of marine subsidies on terrestrial plants: (1) the “fertilization effect,” in which seaweed adds nutrients to plants, increasing their growth rate and possibly their susceptibility to herbivores, and (2) the “predator diet shift effect,” in which lizards shift from eating local prey (including terrestrial herbivores) to eating marine detritivores, leading to increased leaf damage.

Evidence for the fertilization effect comes from higher leaf nitrogen detected in subsidized plots 12 months after adding seaweed (Fig. 2G), coinciding with higher foliage growth measured in subsidized plots after 12 months (Fig. 2H). The lack of such effects prior to this time indicates that several months were required for the nutrients in seaweed to become available for plants. Furthermore, after 12 months we found that some masses of seaweed persisting in subsidized plots contained fine roots from nearby plants. Hence, the fertilization effect may have been slow also because the plants required time to find the subsidized nutrients.

In contrast, the diet shift by predators was rapid. Stable-isotope analysis of lizards sampled after three months indicated that they had shifted to eating more marine-based prey in subsidized plots (Fig. 2C). The dietary shift became more pronounced after six months, even though marine detritivores had declined in subsidized plots at that time (Fig. 2A). The peak response in stable isotopes may have been delayed by the time required for subsidized prey carbon to become lizard tail tissue.

After six months, the percentage of leaf area damaged became significantly higher in subsidized plots (Fig. 2F). The fact that leaf nitrogen was nearly identical in subsidized and removal plots after six months suggests that the higher leaf damage in subsidized plots was not caused by the fertilization effect enhancing plant susceptibility or attractiveness to herbivores. We hypothesize that increased leaf damage was caused, at least in part, by “apparent mutualism” (Abrams and Matsuda 1996) in which lizards switched from eating herbivorous arthropods to marine detritivores. This would reduce predation on herbivores, allowing them to consume more leaf material.

After 12 months, lizard  $\delta^{13}\text{C}$  in subsidized plots declined, coinciding with a decline in leaf damage. This suggests that lizards in subsidized plots switched back to eating more terrestrial herbivores, consequently reducing the percentage of leaf area damaged. However, herbivore abundance tended to be higher in subsidized plots after 12 months. Herbivore abundance may have

increased while leaf damage decreased because foliage growth was higher in subsidized plots (i.e., because there were more new leaves available for herbivores to eat, the mean percentage of each leaf eaten decreased, even though there were more herbivores). Indeed, after 12 months the sum of the areas damaged on all the leaves per branch tended to be higher in subsidized plots ( $54 \pm 14 \text{ cm}^2$  [mean  $\pm$  SE]) than in removals ( $29 \pm 8 \text{ cm}^2$ ), but the difference was not significant ( $P = 0.13$ ). Hence, the causal mechanism for the decline in leaf damage in subsidized plots after 12 months is uncertain.

The overall increase in lizard density during the experiment requires some explanation. We suggest that the rapid numerical response during the first three months was largely caused by lizards aggregating in subsidized plots because *A. sagrei* reproduction is generally low during the fall (Schoener et al. 2004), whereas the increase during the following summer could have been, at least in part, a reproductive response. Because no movement between plots (separated by 10–30 m) by tagged lizards was detected, increased lizard density was probably not caused by lizards migrating from removal to subsidized plots, but rather by lizards moving in from closer areas immediately surrounding the plots. This is consistent with extensive measurements of *A. sagrei* home range sizes (Schoener and Schoener 1982), showing that they are usually much smaller than the area between plots. The experiment began at the end of a two-year drought that was followed by an exceptionally wet year. Therefore, the unexpected rise in removal plots during the course of the experiment may have been linked to increased terrestrial productivity or water availability for lizards; this may explain some of the rise in subsidized plots as well.

Results of the comparative study of natural variation in marine subsidies and terrestrial food web components were consistent with the experimental results. Lizards, herbivorous arthropods, leaf damage, and foliage growth were significantly higher in plots with high subsidies than in those with low subsidies. Although amounts of seaweed added to the experimental plots ( $\sim 2.5 \text{ kg/m}^2$ ) were within the range of those deposited naturally in the comparative plots ( $0\text{--}6.5 \text{ kg/m}^2$ ), the mean amount in the comparative high-subsidy plots was substantially less ( $0.5 \text{ kg/m}^2$ ). Nevertheless, differences in food web components between treatments in the experimental study were similar to differences in food web components between high- and low-subsidy plots in the comparative study. Furthermore, overall values of lizard densities, web spider densities, herbivore relative abundance, leaf damage, and foliage growth were similar in the experimental and comparative studies (compare Figs. 2 and 3). The remarkable congruence of the two studies suggests that the marine subsidy effects produced experimentally occur naturally in this system.

We were surprised that web spiders did not show a significant numerical response to seaweed deposition in our experimental or comparative studies, as found in

previous studies of marine subsidies (Spiller 1992, Polis and Hurd 1995) and freshwater subsidies (Henschel et al. 2001, Kato et al. 2003, Marczak and Richardson 2007, but see Paetzold et al. 2006). We suggest that for Bahamian spiders, the greater negative effect of lizard predation in subsidized plots may counter the positive effect of more food.

We hypothesized that a seasonal pulse of marine subsidies would enhance terrestrial herbivory in the short term (fall and winter) when the predators switch from eating herbivores to detritivores via “apparent mutualism” (Abrams and Matsuda 1996). In the long term (spring and summer), we hypothesized that predators would respond numerically to marine subsidies and then switch back to eating mostly herbivores as the detritivores declined, leading to an “apparent trophic cascade” (Polis et al. 1997) in which subsidies strengthen the positive effect of predators on plants. The experimental results during the first six months, taken together, provide strong support for the hypothesized short-term effect. There are a few hints that the long-term effect was developing in subsidized plots at the end of the year: marine detritivore abundance declined, lizard density remained high, stable-isotope analysis suggested that lizards switched back to eating more terrestrial prey than earlier in the year, and leaf damage decreased. However, another seasonal pulse of seaweed during the following fall would probably cause lizards to shift again to subsidized prey. We suspect that plots with high seaweed deposition in our comparative study may consistently receive relatively high inputs year after year due to topography and orientation of the shoreline and water currents in those areas, and that study also found no evidence for an apparent trophic cascade. Hence, we suggest that the effect of subsidized prey on herbivory followed the apparent mutualism pathway for the following reasons.

First, apparent mutualism is favored when predators become satiated or switch to subsidized prey (Abrams and Matsuda 1996). During the first half of the experiment, lizards may have become satiated on the superabundant subsidized prey. Furthermore, predator switching is facilitated when the alternate prey types occur in different sub-habitats (e.g., Murdoch et al. 1975). This was clearly the case in our study because marine detritivores (mainly amphipods) live in seaweed on the ground whereas herbivorous arthropods occur on foliage above the ground. Similarly, studies of fish foraging in streams on benthic aquatic prey and on surface terrestrial prey support apparent mutualism (Nakano et al. 1999, Baxter et al. 2005).

Second, apparent mutualism is favored when the positive numerical response by predators to subsidized prey is restricted (Holt 1977, Abrams et al. 1998). We suggest that the numerical response by lizards was not strong enough to cause an apparent trophic cascade (via apparent competition) for three reasons: (1) predators of *A. sagrei* (a small lizard), such as snakes, larger lizards,

birds, and rats, were common on the islands in both studies (D. A. Spiller, J. Piovio-Scott, A. N. Wright, L. H. Yang, and G. Takimoto, *personal observations*), (2) intraspecific territoriality in anole lizards is strong (Schoener and Schoener 1982) and may have limited their numerical response, and (3) lizard reproduction was too slow for energy derived from the subsidy to be transformed into substantially more progeny in future generations because the time to maturity is too long and also because lizards are reproductively quiescent from mid-fall to late spring, which includes much of the subsidy period (note the nearly level period in Fig. 2B). In theory, the lack of multiple turnovers of a consumer population during the time interval when the subsidy is available favors apparent mutualism over apparent competition (Takimoto et al. 2009). We suggest that these three factors may be equally important and work together to limit the numerical response by lizards.

Evidence for apparent trophic cascades comes from studies in which the numerical response by predators was more pronounced than in our study. For example, in Polis and Hurd's (1996a) study, web spiders (the focal predators) were six times denser on bushes near shore with marine-based prey subsidies than on bushes further inland without subsidies. In Murakami and Nakano's (2002) study, insectivorous bird activity levels were 5–7 times higher in riparian plots with aquatic prey subsidies than in upland plots. Both of these studies demonstrated that the top-down effect of predators on herbivores was stronger in subsidized areas, supporting the apparent cascade effect. In our studies mean lizard density was only 1.6 times higher in subsidized than removal plots at the end of the experiment and was only 1.4 times higher in comparative plots with high subsidies than in those with low subsidies. Similarly, the numerical response by predators was relatively weak in other studies failing to uncover evidence of an apparent cascade (Sabo and Power 2002b, Miyashita et al. 2003, Birkhofer et al. 2007). Experiments by Halaj and Wise (2002) and Henschel et al. (2001) both showed a moderate numerical response by spiders to subsidized prey (two- to threefold increase), but only the latter study supported the apparent cascade effect.

In addition to the indirect effects of subsidized detritivore prey, we found evidence for a direct positive effect of seaweed on plants: the fertilization effect. Similarly, studies of seabirds and salmon carcasses show that these marine subsidies provide nutrients for terrestrial plants as well as food for terrestrial consumers (Anderson and Polis 1998, Wilson et al. 2004, Bartz and Naiman 2005, Fukami et al. 2006). Croll et al. (2005) and Maron et al. (2006) showed that by preying on seabirds, foxes reduced the amount of marine-derived nutrients on Aleutian Islands, which in turn transformed plant communities from grasslands to shrubs and forbs. Multiple effects produced by a single detrital resource may be common in other systems as well. Studies of periodical cicadas showed that carcasses in streams

subsidize both aquatic producers and consumers (Nowlin et al. 2007). Addition of cicada carcasses in forest plots increased detritivorous, omnivorous, and predaceous arthropods, increased microbial biomass in soil, increased growth and reproduction in understory plants, and increased herbivory on plants (Yang 2004, 2006, 2008); the latter effect appeared to be caused by the selective foraging of mammalian herbivores on plants that were fertilized by carcasses, rather than by the predator diet shift effect uncovered in the present experiment. Hence, the present study complements others showing that detrital resource inputs can produce multiple effects that cascade up and down food webs (Polis and Strong 1996, Wardle 2002, Moore et al. 2004).

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#### APPENDIX A

Estimated biomass of arthropods collected in bowl traps (*Ecological Archives* E091-099-A1).

#### APPENDIX B

Stable-isotope analysis of lizard tails, leaves, and seaweed, and estimation of percentage of marine-based prey consumed by lizards using mixing models (*Ecological Archives* E091-099-A2).

#### APPENDIX C

Estimated biomass of seaweed naturally deposited on shoreline plots (*Ecological Archives* E091-099-A3).

## APPENDIX A. Estimated biomass of arthropods collected in bowl traps.

Biomass of amphipods was estimated using a length-weight power equation derived by measuring under a dissecting microscope with an ocular micrometer the length of 20 different-sized amphipods which were then dried and weighed (Fig. A1). Amphipod biomasses collected in plots with seaweed added and removed are in the manuscript (Fig. 2A). Other arthropods were estimated using published taxon-specific length-weight power equations. The sources for each taxon are as follows. Schoener (1980, tropical dry forest): Diptera (adults), Lepidoptera, Orthoptera, Coleoptera, Formicidae, Hymenoptera (Formicidae excluded), Hemiptera, Homoptera. Gowing (1984): Araneae, Chilopoda, Isopoda. Ganihar (1997): Dermaptera, Thysanura. Caballero et al. (2004): Collembola (Entomobyidae). Rogers et al. (1977): Diptera (larvae). Biomasses of the seven taxon with the highest cumulative total (across all plots and dates) are in Fig. A2.

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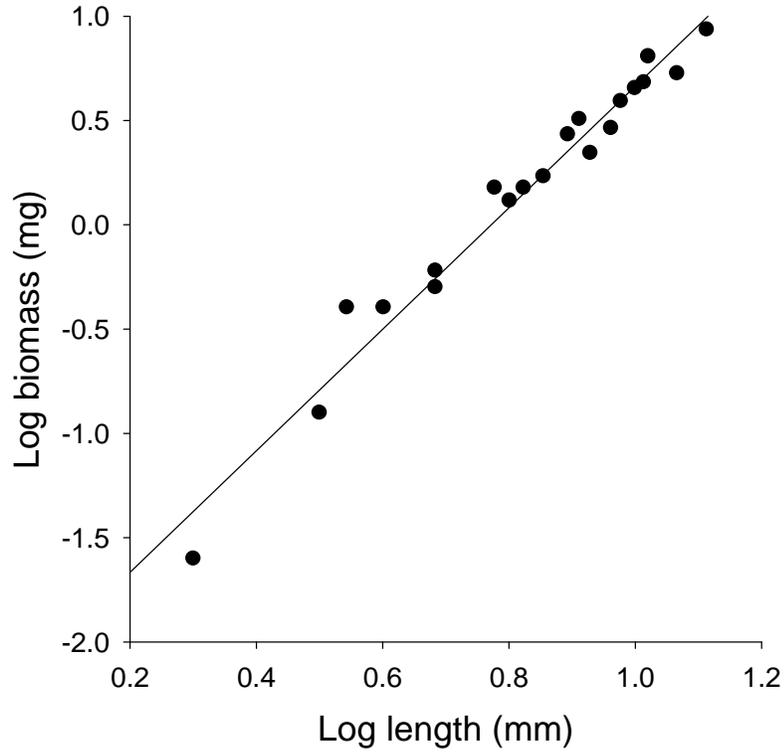


Fig. A1. Log-log relationship between length and biomass of amphipods (*Tethorchestia* spp.).

The regression equation is  $\log(\text{biomass}) = -2.249 + 2.914 \log(\text{length})$  which was transformed to  $\text{biomass} = 0.006 \text{ length}^{2.914}$ .

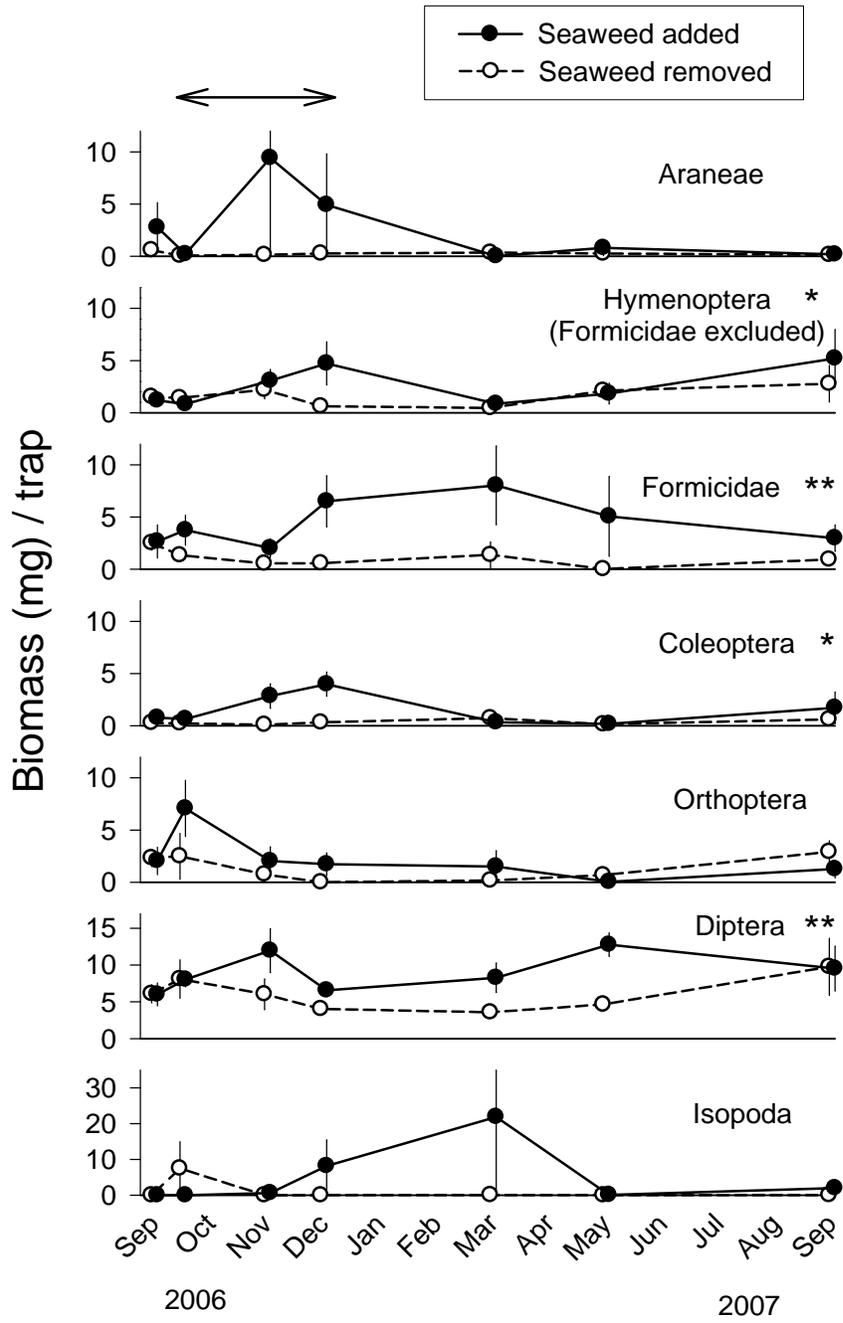


Fig. A2. Mean biomasses of arthropods collected in bowl traps in plots with seaweed added and removed. Arrows denote the manipulation period. Error bars are  $\pm 1$  SE. Repeated measures, overall treatment effect on post-manipulation dates: \*  $P < 0.05$ , \*\*  $P < 0.01$ .

## APPENDIX B. Stable isotope analysis

*Sample preparation and analysis*

Lizard tails, terrestrial plant leaves, and seaweed were dried at 55 °C for 48h. Plant leaves and seaweed were ground to fine powder. Lipids were extracted from tail tips using methanol-chloroform (2:1 by volume). Isotope and leaf nitrogen content analysis was performed with a continuous-flow isotope ratio mass spectrometry using an ANCA-GSL elemental analyzer interfaced to a GEO 20-20 IRMS (Sercon Ltd., Cheshire, UK) at Faculty of Engineering at University of Yamanashi, Japan. The standard deviation of replicates of organic standard was 0.14‰ for  $\delta^{13}\text{C}$ . All stable-isotope values were reported in the  $\delta$  notation:  $\delta^{13}\text{C} = ([^{13}\text{C}/^{12}\text{C}_{\text{sample}} / ^{13}\text{C}/^{12}\text{C}_{\text{standard}}] - 1) \times 1000$ . No significant difference in  $\delta^{13}\text{C}$  was found between the tail and whole body of the Anolis lizards (Takimoto et al. 2008).

*Baseline values and mixing models*

To obtain baseline values for terrestrial and marine resources, we conducted carbon stable isotope analysis on samples of leaves and seaweed collected in each experimental plot. Baseline  $\delta^{13}\text{C}$  values did not differ significantly between treatments (Fig. B1; overall treatment effect in repeated measures ANOVA on terrestrial plants,  $F_{1,5} = 0.25$ ,  $P < 0.64$ ; on seaweed,  $F_{1,5} = 0.89$ ,  $P < 0.39$ ). These values were used in a simple mixing model (Post 2002) which estimates the percentage of marine-based prey consumed by lizards in each plot as follows: % Marine diet =  $100((\delta^{13}\text{C}_L - \Delta_C) - \delta^{13}\text{C}_T) / (\delta^{13}\text{C}_S - \delta^{13}\text{C}_T)$ , 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, and  $\Delta_C$  is the trophic fractionation of carbon. There is some debate over carbon fractionation. Post (2002)

found that it was minimal ( $\sim 0$ ) but more recent studies found that it can be substantial for herbivorous insects (McCutchan et al. 2003, Langellotto et al. 2005, Mooney and Tillberg 2005, Spence and Rosenheim 2005). We conducted stable isotope analysis on *Conocarpus erectus* leaves and herbivorous beetles collected on *C. erectus* leaves from 3 different islands. Mean  $\delta^{13}\text{C}$  values were 3.0 to 4.6 units higher for beetles than for leaves (Fig. B2). We used the average difference (3.8 units) as  $\Delta_C$  in the mixing model which assumes that fraction of all terrestrial lizard prey is this value and no fractionation in marine prey or in lizards. We also computed estimates using the same mixing model but with no fractionation ( $\Delta_C=0$ ). The results show that the difference between treatments is very similar with and without fractionation, except the estimates of percent marine-based diets are higher for the model without fractionation (Fig. B1); this pattern is very similar to that of the raw  $\delta^{13}\text{C}$  values for lizards presented in the manuscript (Fig. 3C). Results of the model with fractionation are obviously better because some estimates in the model without fractionation were greater than 100%. Estimates with fractionation are reasonable but we caution that they may be inaccurate due to a lack of information on all of the potential sources of prey in the lizard diets. The main purpose of this presentation is to verify that there was indeed a shift in the lizard diets in the subsidized plots even when accounting for variation among plots in the baseline isotopic values.

#### *Results of stable isotope analysis of all plots*

One of the three experimental islands was omitted from the analysis given in the manuscript because it did not have at least 3 lizards in each plot during the first half of the experiment; we opted to present the results for only the other two islands for which we had a complete time series of data, as we did for all of the other response variables. Lizards became

more abundant on all islands during the second half of the experiment. Here we present the data for all plots during this period. In May and Sept. 2007, lizard  $\delta^{13}\text{C}$  values were significantly higher in subsidized plots than in removals (Fig. B3).

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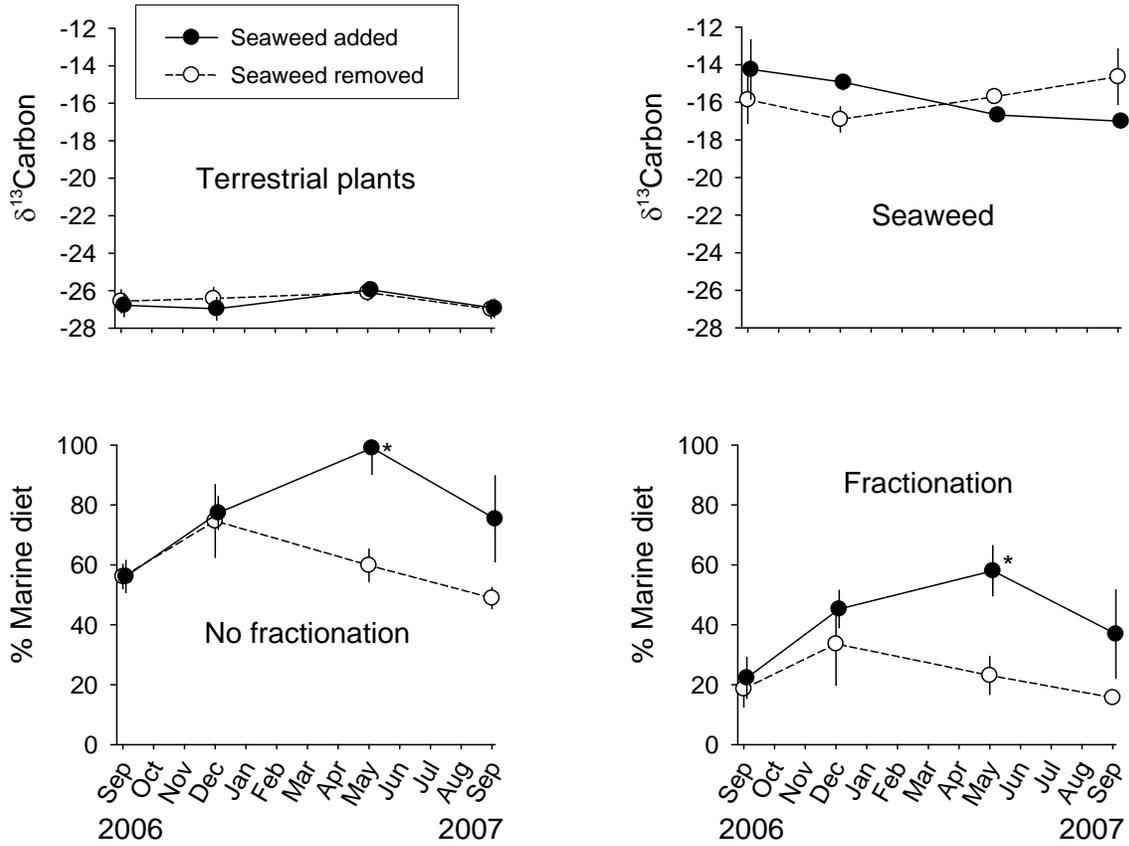


Fig. B1. Carbon stable isotope analysis of terrestrial plants and seaweed and estimates of percentage of marine prey in lizard diets in experimental plots with seaweed added and removed (mean  $\pm 1$  SE). \*  $P < 0.05$ , significant within-date ANOVA treatment effect (stepdown Bonferroni adjusted).

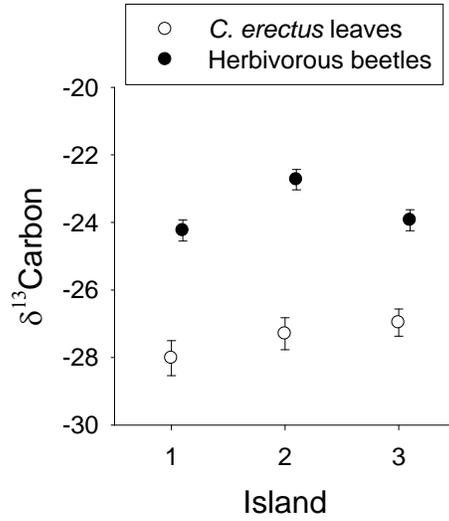


Fig. B2. Carbon stable isotope analysis of *C. erectus* leaves and herbivorous beetles collected on three different islands. Symbols and bars are the means  $\pm 1$  SE.

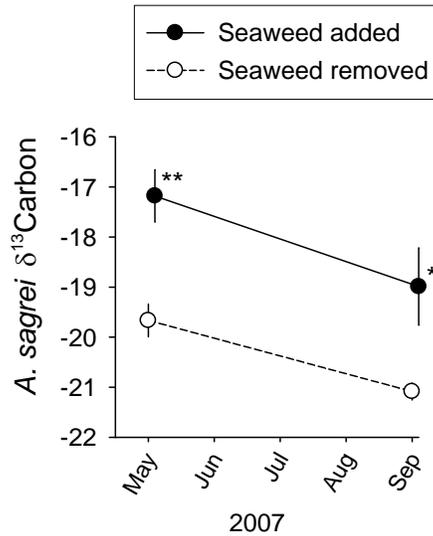


Fig. B3. Carbon stable isotope analysis of lizard diets in experimental plots with seaweed added and removed (mean  $\pm 1$  SE). Significance level of within-date ANOVA treatment effect (stepdown Bonferroni adjusted): \*  $P < 0.05$ , \*\*  $P < 0.05$ .

## APPENDIX C. Estimated biomass of seaweed naturally deposited on shoreline plots

Seaweed biomass present on 29 study plots was visually estimated. To calibrate our estimates, we visually estimated seaweed present in 21 areas outside the study plots and then collected and weighed the seaweed; visual estimates were highly correlated with measured amounts ( $r = 0.96$ ,  $P < 0.001$ , Fig. C1). Study plots were divided into two categories: high subsidies ( $>1$  kg mean biomass of seaweed present averaged over the three censuses,  $n=11$ ) and low subsidies ( $\leq 1$  kg,  $n=18$ ). Estimates for each plot recorded in Sept., Nov. and Dec. 2007 are in Fig. C2. Note that all plots designated to the high subsidy category had consistently more seaweed than those designated to the low subsidy category.

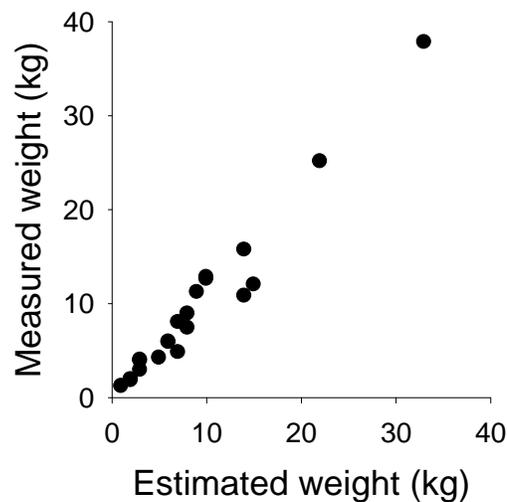


Fig. C1. Measured and estimated wet weight of seaweed in 4 m<sup>2</sup> plots.

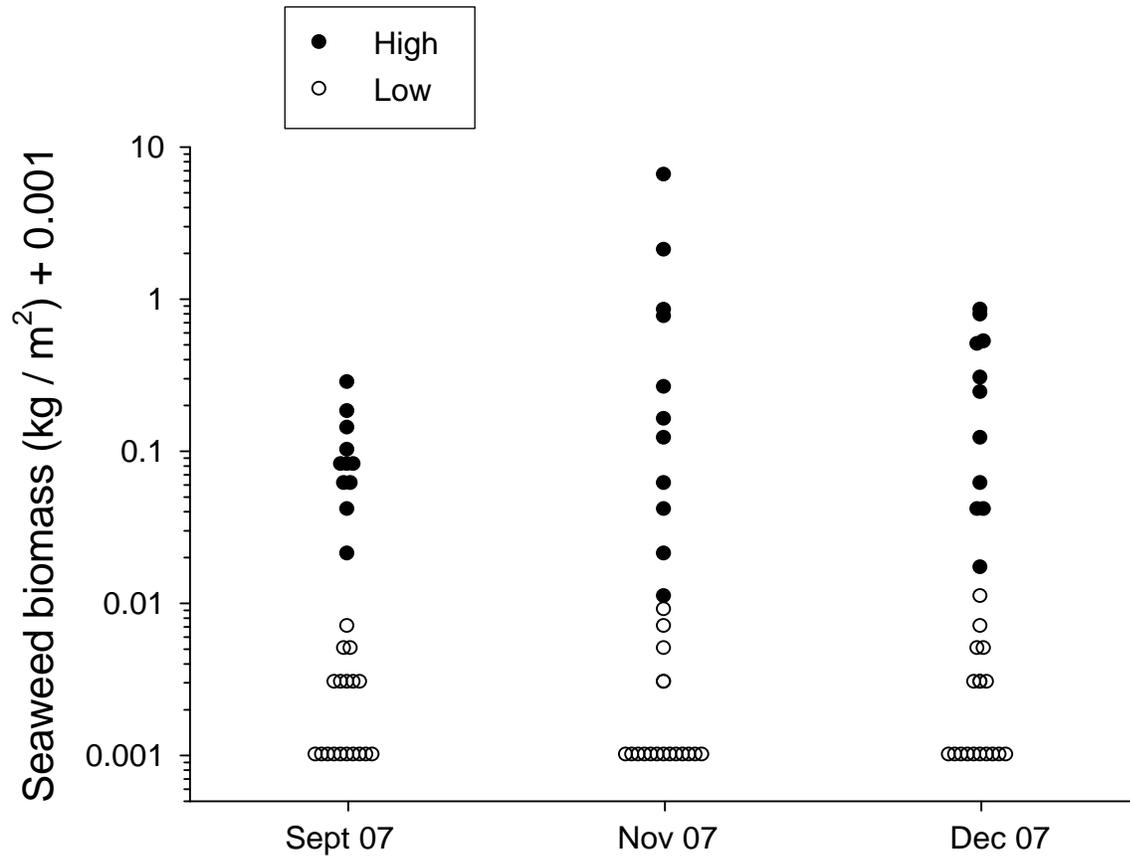


Fig. C2. Biomass of seaweed estimated in high and low deposition plots.