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Title: Pulsed seaweed subsidies drive sequential shifts in the effects of lizard predators on island food webs

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33**Abstract**

34Most prominent theories of food-web dynamics imply the simultaneous action of

35bottom-up and top-down forces. However, transient bottom-up effects resulting

36from resource pulses can lead to sequential shifts in the strength of top-down

37predator effects. We used a large-scale field experiment (32 small islands sampled

38over 5 years) to probe how the frequency and magnitude of pulsed seaweed inputs

39drives temporal variation in the top-down effects of lizard predators. Short-term

40weakening of lizard effects on spiders and plants (the latter via a trophic cascade)

41were associated with lizard diet shifts, and were more pronounced with larger

42seaweed inputs. Long-term strengthening of lizard effects was associated with lizard

43numerical responses and plant fertilization. Increased pulse frequency reinforced

44the strengthening of lizard effects on spiders and plants. These results underscore

45the temporally variable nature of top-down effects and highlight the role of resource

46pulses in driving this variation.

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48

49**Introduction**

50It has long been recognized that bottom-up forces play a key role in determining the 51strength of top-down control in food webs. Inquiries into this relationship have often 52assumed that food webs are close to equilibrium conditions, and that bottom-up and 53top-down forces act simultaneously (Oksanen *et al.* 1981; Leroux & Loreau 2015), 54but food webs in nature are often characterized by transient processes, such as 55responses to disturbance and seasonal reassembly (e.g., Power *et al.* 1996, 2008; 56Nakano & Murakami 2001; McMeans *et al.* 2015; Spiller *et al.* 2018). Resource pulse 57theory, which has recently emerged as an influential non-equilibrium approach to 58understanding the consequences of transient bottom-up effects (Ostfeld & Keesing 592000; Holt 2008; Yang *et al.* 2008, 2010; Hastings 2012), suggests that bottom-up 60and top-down effects often occur sequentially, rather than simultaneously. 61However, few experimental studies have evaluated how resource pulses drive 62change in the strength of top-down control. Moreover, recent syntheses of empirical 63research on resources pulses called for studies that evaluate how the magnitude 64and frequency of resource pulses influence ecological responses, including changes 65in the strength of top-down control (Yang *et al.* 2008, 2010; Richardson & Sato 662015).

67Resource pulses are brief periods of unusually high resource availability (Yang *et al.* 682008). When these resource pulses are transported across space, the dynamics of 69resource input are usually decoupled from those of the recipient food web (i.e., they 70are donor-controlled) (Polis *et al.* 1997). Such pulsed subsidies (sensu Yang *et al.* 712008) are thought to elicit sequential shifts in top-down predator effects on local 72food-webs through three primary pathways: 1) changes in predator diet, 2) predator 73numerical responses (which can be driven by both aggregation and reproduction),

74and 3) fertilization of primary producers (Yang *et al.* 2008, 2010; Takimoto *et al.*

752009; Leroux & Loreau 2012). Shifts in predator diet can emerge rapidly, and are

76likely to reduce top-down effects on non-pulsed resources via apparent mutualism

77(Abrams & Matsuda 1996; Abrams 2010), as resident predators reorient their diet

78and foraging behavior towards the pulsed resource (Ostfeld & Keesing 2000; Yang

79*et al.* 2008, 2010; Leroux & Loreau 2012). Numerical responses, which are expected

80to strengthen top-down effects on local resources via apparent competition (Holt

811977; Holt & Lawton 1994), can emerge rapidly due to aggregation (e.g., Murakami

82& Nakano 2002), but time lags can delay the reproductive component of the

83numerical response (Holt 2008; Yang *et al.* 2010). Fertilization associated with

84nutrient subsidies is expected to strengthen top-down effects of predators on

85plants, as increases in both primary productivity and the nutritional quality of plant

86material often magnify herbivore pressure in the absence, but not the presence, of

87predators (Oksanen *et al.* 1981; Polis 1999; Leroux & Loreau 2008). However, if

88pulsed subsidies need to undergo decomposition prior to uptake by primary

89producers (e.g., Spiller *et al.* 2010), these effects may be delayed. Thus, existing

90theoretical and empirical evidence suggests a sequential shift in top-down effects:

91pulsed subsidies are likely to weaken top-down predator effects on the local food

92web initially but should subsequently strengthen them (Ostfeld & Keesing 2000;

93Yang *et al.* 2008, 2010; Leroux & Loreau 2012) (Fig. 1a).

94The hypothesized sequential shift between weakened and strengthened top-down

95effects (Fig. 1a) could be influenced by the magnitude and frequency of pulsed

96subsidies. An increase in the magnitude of subsidies can lead to a quantitative

97change in the impact of pulsed subsidies, without changing the temporal pattern of

98effects (e.g., Yang *et al.* 2010; Leroux & Loreau 2012). Alternatively, increases in

99subsidy magnitude can lead to qualitative changes in predator effects by 100restructuring food webs (e.g., Klemmer & Richardson 2013) or, in models with 101constant subsidy input, causing numerical responses to overwhelm diet shifts 102(Leroux & Loreau 2012). Changes in pulse frequency can also lead to quantitative 103and qualitative changes in top-down effects (Takimoto *et al.* 2009; Leroux & Loreau 1042012). For example, frequent pulses might lead to simultaneous behavioral and 105numerical responses that cancel each other out, which could result in no net change 106in top-down effects (Takimoto *et al.* 2009; Dreyer *et al.* 2016). Alternatively, 107compounding consumer numerical responses (e.g., Leroux & Loreau 2012; Gratton 108*et al.* 2017) may increase the magnitude and duration of enhanced top-down 109effects. In this study, we use a large-scale field experiment to probe how the 110frequency and magnitude of pulses of seaweed deposition influence the top-down 111effects of lizard predators on island food webs.

112Bahamian islands have served as a model system for investigations of top-down 113effects in food webs. Brown anoles (*Anolis sagrei* Dumeril & Bibron, hereafter 114lizards) are the most common vertebrate predator on small islands and have been 115shown to have strong direct effects on arthropods such as web spiders (e.g., 116Schoener & Spiller 1996) and salticid spiders (Piovia-Scott *et al.* 2017), and 117herbivore-mediated indirect effects on plants such as buttonwood (*Conocarpus* 118*erectus* L.) via a trophic cascade (e.g., Schoener & Spiller 1999) (Fig. 1b). Seaweed 119deposition also has profound effects on these island food webs. Seaweed is 120frequently deposited in pulses, and experimental seaweed pulses rapidly elicited 121changes in the foraging behavior (Kenny *et al.* 2017) and diet (Spiller *et al.* 2010) of 122resident lizards. These shifts towards marine-derived prey may increase herbivory 123on terrestrial plants by reducing predator pressure on herbivores (Spiller *et al.*

1242010; Piovia-Scott *et al.* 2011) (Fig. 1c). Notably, the lizard diet shift is relatively

125short-lived, being undetectable within a year after seaweed was added. Lizard

126numerical responses to seaweed subsidies can occur rapidly due to aggregation

127(Spiller *et al.* 2010), but reproductive contributions to numerical responses tend to

128take at least a year to develop (Wright *et al.* 2013), as do fertilization effects (Spiller

129*et al.* 2010). While there is evidence from an observational study that chronic

130seaweed deposition can increase the long-term top-down effects of lizards through

131numerical responses (Piovia-Scott *et al.* 2013) (Fig. 1d), the impact of different

132seaweed pulse regimes on temporal variation in top-down effects has not been

133experimentally investigated in this system.

134In the current study, we manipulated the frequency and magnitude of pulses of

135seaweed deposition on small islands with or without experimentally introduced

136populations of lizards. The experiment included 32 small islands and took place over

137the course of five years. In addition to controls with no seaweed addition, the

138experiment featured three seaweed-addition treatments: 1) a 'single large'

139seaweed pulse in the first year of the experiment, 2) 'several small' pulses, in which

140three smaller seaweed pulses were added in each of the first three years of the

141experiment (the cumulative amount deposited was the same as in the single large

142treatment), and 3) 'several large' pulses, in which each of the three annual seaweed

143pulses was the size of the single large pulse. Comparisons between lizard and no-

144lizard islands in the seaweed treatments allow us rigorously to evaluate hypotheses

145about how different patterns of seaweed deposition change the food-web effects of

146lizards. Our central hypothesis was that there would be a sequential shift in top-

147down effects; compared to no-seaweed controls, a pulse of seaweed deposition

148would first weaken the top-down effects of lizards on terrestrial arthropods and

149plants (due to changes in foraging behavior and diet), then enhance these effects
150due to lizard numerical responses and plant fertilization effects (the latter is
151expected to increase the cascading effects of lizards on plants). Because the
152experimental islands are too isolated for significant aggregative responses, we did
153not expect a numerical response to occur in the first year of the study. In addition to
154this central hypothesis, we also investigated how altering the frequency and
155magnitude of pulsed seaweed subsidies affected the strength of top-down effects.
156We predicted that larger pulsed subsidies would increase the magnitude of
157alterations in top-down effects, but not the qualitative temporal pattern (weakening
158followed by strengthening) of those alterations, as we did not expect changes in the
159time lags associated with reproductive responses or significant restructuring of the
160food web. Furthermore, we predicted that increased frequency of pulsed subsidies
161would have compounding effects on lizard numerical responses, as the annual
162pulsed subsidies coincided with an important developmental window (Wright *et al.*
1632013), increasing the long-term strength of top-down effects.

164**Material and methods**

165*Study system and experimental design*

166We conducted our study on small islands adjacent to the much larger island of
167Great Abaco, Bahamas. The most common components of the food webs on these
168islands include perennial shrubs (of which buttonwood [*Conocarpus erectus*] is
169among the most common), various arthropods (primarily insects, arachnids, and
170crustaceans), and the predaceous lizard *Anolis sagrei* (the brown anole), which is
171the most abundant terrestrial vertebrate in this ecosystem.

172In order to evaluate the effect of pulsed subsidies on the top-down effects of lizard 173predators we conducted a seaweed-addition experiment on (1) islands on which we 174experimentally introduced lizard populations (hereafter lizard islands) and (2) no-175lizard control islands (hereafter no-lizard islands). Our study featured four seaweed 176treatments, each of which was applied to four lizard and four no-lizard islands for a 177total of 32 islands: 1) single large: a large pulse of seaweed (2.5 kg m^{-2}) added in 178the first year of the study, 2) several small: a small pulse of seaweed (0.83 kg m^{-2}) 179added in each of the first three years of the study (resulting in the same total 180amount of subsidy as treatment 1), 3) several large: a large pulse of seaweed (2.5 181kg m^{-2}) added in each of the first three years of the study, and 4) no-seaweed 182control: no seaweed added for the duration of the study (Figs. S1, S2; Table S1). The 183large pulses are consistent with naturally-occurring seaweed deposition events 184(Spiller *et al.* 2010). Background seaweed deposition rates on the experimental 185islands were generally much smaller in magnitude than our seaweed manipulations 186(mean: 0.076 kg m^{-2}, maximum: 0.45 kg m^{-2}; Table S1), in part because the study 187islands were located in a protected creek area.

188To assign lizard and seaweed treatments to islands, we first divided the 32 study 189islands into four blocks of eight islands based on vegetated area. We then ordered 190the eight islands in each block by vegetated area, randomly selected the first one 191as either lizard introduction or lizard control, then alternated the two lizard 192treatments (i.e., lizard treatment assignment was stratified by vegetated area, our 193metric of island size). Finally, we randomly assigned each of the four seaweed 194treatments to the four lizard-introduction islands and four lizard control islands in 195each block.

196Lizard introductions were initially conducted in May 2012, and the first seaweed

197additions were conducted in September 2012. However, Hurricane Sandy hit our

198study site on October 26, 2012, eliminating all of the experimental lizard

199populations and washing away all of the experimental seaweed deposits. Because

200of this, we re-established the lizard populations and seaweed treatments in

201December, 2012. In 2013, 2014, and 2015, we visited the field site and collected

202data in late spring (May), early fall (September/October), and late fall/early winter

203(December/January). Our final sampling trip was May 2016. One of the no-lizard

204control islands (X01) became colonized by lizards partway through the experiment

205as a result of a natural colonization event. Because of this, we did not include data

206from this island collected after May 2014 in our analyses.

207*Data collection*

208We censused web spiders by counting all intact webs on each study island. Web

209spider abundance was calculated as the number of intact webs per square meter of

210vegetated area. We estimated salticid spider abundance using two methods: 1)

211bowl traps, and 2) tap samples. For the bowl traps, plastic bowls were filled with

212500 mL of water and a few drops of detergent, and collected after 24 hours

213(approximately one bowl was set for every 15 m^2 of vegetated area), following the

214methods of Piovia-Scott et al. (2017). For the tap sampling, we placed a plastic tray

215under a section of buttonwood branch (approximate volume: 0.125 m^3) and tapped

216or shook the foliage, catching all dislodged arthropods in the tray; this was repeated

217three times on each island. Salticid spider abundance was calculated as the number

218of salticids per bowl trap plus the number of salticids per tap sample.

219For plant data collection, we selected one to four buttonwood plants on each island

220in May 2012. On each of these plants, we collected data on growth by measuring

221shoot elongation on four actively-growing stems on each plant. On each sampling

222trip, the most apical leaves on each selected stem were marked with ink. During the

223following trip, we measured the length of shoot elongation that occurred beyond the

224marked leaves and calculated shoot elongation in mm day^{-1}. We collected data on

225herbivory by measuring leaf damage during each sampling trip. To measure leaf

226damage we haphazardly collected 10 leaves from each plant, then pressed and

227photographed these leaves. We conducted image analysis of the resulting images,

228using ImageJ (Schneider *et al.* 2012) to measure the total leaf area and the

229damaged area; we then calculated % leaf damage. At the beginning of the study we

230collected individual plant data to use as covariates in analyses: to estimate plant

231size (volume) we measured the height, width, and breadth and assumed an ellipsoid

232shape; after Hurricane Sandy, we also estimated the degree to which each plant

233was damaged by the hurricane by calculating the proportion of marked stems that

234were killed by the storm. Finally, we used island height as a covariate in our

235analyses of plant data. This was measured as the vertical distance from the high

236water line to the highest point of ground on the island.

237*Statistical analysis*

238Our general analytical approach was to fit linear mixed models (LMMs) using log-

239transformed response variables, then use planned contrasts to evaluate how the

240seaweed treatments changed the effect of lizards on plants and spiders. All LMMs

241included seaweed treatment, lizard treatment (introduced vs. absent), and their

242interaction as fixed effects, and experimental block and island as random effects;

243we used the plant- and island-level covariates described above for analyses of leaf

244damage and shoot growth and pre-treatment baseline data as a covariate in

245analyses of leaf damage and web spider density (see below and Appendix S1 for

246details).

247Our primary planned contrasts were designed to compare the effect of lizards in

248each of the three seaweed-addition treatments to that in the no-seaweed control

249treatment. For the LMMs these contrasts are analogous to differences between the

250log of the lizard response ratio (a common measure of effect size) in each seaweed

251treatment vs. the no-seaweed controls, as the response variables were log-

252transformed prior to analysis (Appendix S1). We also used specific contrasts to

253evaluate how the strength of lizard effects was influenced by pulse magnitude (i.e.,

254comparing seaweed-addition treatments with different amounts of seaweed added)

255and frequency (i.e., comparing lizard effects in the several large and several small

256treatments to those in the single large treatment) (see Appendix 1 for details).

257We took two different approaches to evaluating how the influence of seaweed

258addition on lizard effects changed over time: 1) short-term vs. long-term (in which

259each of these time periods encompassed multiple sampling trips), and 2) trip-

260specific (i.e., repeated-measures analyses in which each sampling trip is considered

261a time point). In general, short-term effects included data collected prior to the

262second seaweed addition (i.e., May 2013 and September 2013 sampling trips),

263which occurred 9 months after the initial seaweed addition. Long-term effects

264included all time points after September 2013, as these time points were expected

265to include lizard numerical responses (Wright et al. *in review*) as well as the effects

266of subsequent seaweed additions (in the several large and several small

267treatments). Exceptions to the general approach described above are provided in

268the next paragraph; a more detailed account of the statistical methods can be

269found in Appendix S1.

270For the two plant response variables (leaf damage and shoot growth), short-term

271effects were based on the September 2013 sampling trip only, as the aftereffects of

272Hurricane Sandy still had a major effect on plant variables in May 2013. Also, the

273long-term analysis of shoot-growth featured cumulative shoot growth on each plant

274after September 2013 as a response variable, instead of maintaining separate

275observations from each sampling period. Because our data on salticid spiders did

276not conform to the assumptions of LMMs, and more sophisticated model structures

277did not provide satisfactory convergence of the model-fitting algorithms, we used a

278randomization analysis for that response variable that incorporated the same basic

279design elements as our LMMs (Appendix S1).

280All hypotheses were evaluated using two-tailed hypothesis tests with $\alpha=0.05$. All

281analyses were conducted in R v 3.4.3 (R Core Team 2017). Linear mixed models

282were fit using functions from the 'lme4' package (Bates *et al.* 2015), contrasts for

283LMMs were evaluated using the 'emmeans' package (Lenth 2018), and

284permutations for the non-parametric analyses were conducted using the 'permute'

285package (Simpson 2016). Raw data and code for all analyses are archived on Dryad

286(doi:10.5061/dryad.bs449c6). All models were consistent with assumptions of

287normality of residuals and homoscedasticity, except where noted.

288**Results**

289*Sequential changes in the lizard effect*

290For all response variables, seaweed addition tended to be associated with relatively

291weaker short-term lizard effects and relatively stronger long-term lizard effects

292(Figs. 2-5). The strength of statistical support for this pattern, and the extent to

293which lizard effects in the seaweed addition treatments were statistically

294distinguishable from no-seaweed controls varied by response variable and seaweed

295treatment (Figs. 2, 3; details below and in Appendix 1).

296We observed short-term reductions in the strength of top-down effects of lizards

297compared to controls when large amounts of seaweed were added for web spider

298abundance (*lizard effect in several large vs. control*: t=4.03, df=50.0, p<0.001) and

299buttonwood shoot growth *(lizard effect in several large vs. control*: t=2.09,

300df=386.6, p=0.037) (Fig. 2). This pattern was also observed for web spider

301abundance in the several small treatment (*lizard effect in several small vs. control*:

302t=2.52, df=51.1, p=0.004; Fig. 2). Trip-specific analyses showed that reductions in

303the lizard effect on web spider abundance were most pronounced in May 2013 (Figs.

3043, 4; Table S3). This short-term weakening of the lizard effect in response to a

305seaweed pulse was not observed for salticid spiders (p>0.25 in all analyses) or leaf

306damage (p>0.15 in all analyses) (Fig. 2; Table S3).

307We found long-term increases in the strength of lizard effects in the several large

308treatment compared to controls for cumulative buttonwood shoot growth (*lizard

309effect in several large vs. control*: t=2.14, df=16.05, p=0.048), and a marginally

310significant trend in the same direction for leaf damage (*lizard effect in several large

311vs. control*: t=1.9, df=23.8, p=0.069) (Fig. 2). Trip-specific analyses showed

312enhanced lizard effects on shoot growth in the several large treatment in October

3132015, and enhanced lizard effects on leaf damage in December 2013 (several large)

314and May 2014 (several large and several small) (Figs. 3, 5; Table S3).

315Our non-parametric analyses also showed long-term increases in the strength of
316lizard effects on salticids in the several small treatment (*lizard effect in several*
317*small vs. control* [*permutation analysis*]: p=0.008; Fig. 2), but this did not occur in
318the other two seaweed treatments (p>0.4 in both cases). Trip-specific analyses
319showed enhanced lizard effects on salticids in the several small treatment in May
3202016 (Figs. 3, 4; Table S3). In contrast to salticids, the negative effects of lizards on
321web spider abundance was weaker than that on controls in the several large
322seaweed treatment, though the trend was marginally significant (*lizard effect in*
323*several large vs. control*: t=1.26, df=23.1, p=0.059) (Fig. 2). Trip-specific analyses
324showed a significant reduction in the lizard effect on web spiders in the several
325large treatment in October 2015 and the several small treatment in September
3262014 (Figs. 3, 4; Table S3).

327*Pulsed subsidy magnitude and lizard effects*

328There was a marginally significant tendency for larger pulsed subsidies to elicit
329greater short-term reductions in lizard effects on shoot growth and salticid spiders
330in the several large and single large seaweed treatments than in the several small
331seaweed treatment (Table S4; Fig. 2). There was not strong statistical support for
332differences in long-term lizard effects between the several large treatment and the
333several small or single large treatment (p>0.11 in all cases; Fig. 2).

334*Pulsed subsidy frequency and lizard effects*

335The negative effects of lizards on salticids were stronger in the several small
336treatment than the single large treatment over the course of the experiment,
337whereas there were no differences between these two treatments for the other
338response variables (Figs. 3, 5; Table S5). After the second seaweed addition lizard

339effects on leaf damage were stronger in the several large and several small

340treatments than in the single large treatment (Figs. 3, 5; Table S6).

341

342**Discussion**

343*Do pulsed subsidies first weaken, then strengthen top-down effects?*

344Predator diet shifts are expected to drive short-term weakening in top-down effects

345on local resources, while predator numerical responses and plant fertilization effects

346are expected to lead to long-term strengthening of top-down effects. As

347hypothesized (Fig. 1), we found multiple instances of short-term reductions in the

348strength of top-down effects of lizards following a pulse of seaweed deposition (Fig.

3492). In the first year after seaweed addition, the effect of lizards on web spiders and

350buttonwood growth was reduced compared to islands with no seaweed added in the

351several large treatment (Fig. 2). We also found multiple instances of the

352hypothesized strengthening of top-down effects of lizards over longer time periods.

353Compared to no-seaweed islands, lizards had stronger long-term positive effects on

354plant growth when several large pulses of seaweed were added and stronger

355negative effects on salticids when several small pulses of seaweed were added (Fig.

3562). These effects of seaweed addition are consistent with our general prediction.

357Plant growth was the only one of the four response variables that showed the

358hypothesized switch from significantly weakened effects in the short-term to

359significantly strengthened effects in the long-term, though a similar trend was

360evident for all response variables (Fig. 2). Thus, we found support for the hypothesis

361that pulsed seaweed subsidies first weaken, then strengthen a lizard-initiated

362trophic cascade involving herbivores and buttonwood plants.

363This sequential weakening, then strengthening in trophic cascade strength is likely

364driven by the differences in the timing of diet shifts, numerical responses, and

365fertilization effects. A pulse of seaweed deposition can lead to a rapid lizard diet

366shift (Spiller *et al.* 2010; Kenny *et al.* 2017, Wright et al. in review), which likely

367reduces lizard effects on herbivores, resulting in increased herbivore effects on

368plants and a weaker effect of lizards on plant growth (Fig. 1c). A similar short-term

369weakening of top-down effects in response to pulsed subsidies has been shown in

370other systems (e.g., Nakano *et al.* 1999; Sabo & Power 2002; Sato *et al.* 2012), and

371is predicted to occur in short-term studies in which consumers display rapid shifts in

372foraging behavior, but slow reproductive responses (Takimoto *et al.* 2009; Leroux &

373Loreau 2012), as in our system.

374Long-term increases in the strength of top-down lizard effects could result from: 1)

375lizard numerical responses, and 2) increased plant growth potential resulting from

376fertilization by seaweed-derived nutrients (Fig. 1d). Numerical responses to pulsed

377subsidies are expected to be associated with stronger lizard effects because higher

378lizard densities more effectively suppress prey. Fertilization is expected to drive

379stronger trophic cascades due to increased quantity and quality of foliage for

380herbivores, leading to increased herbivory on no-lizard islands, but not on islands

381with lizards, which control herbivore abundance. Seaweed deposition was

382associated with higher lizard abundance (i.e., a numerical response; Wright et al, *in*

383*review*) and higher plant growth rate (Piovia-Scott *et al.*, unpublished analysis) in

384our experiment, suggesting that both pathways could be involved in strengthening

385lizard effects. However, a comparative study of chronic seaweed inputs by Piovia-

386Scott et al. (2013) showed that over long periods of consistent seaweed deposition

387the bottom-up fertilization effects of seaweed on leaf damage overshadowed top-

388down effects mediated by lizard abundance. Thus, we suggest that the fertilization

389pathway is a stronger driver of increased trophic cascade strength than the lizard

390numerical response. Other empirical studies have shown that pulsed subsidies

391enhance top-down effects (e.g., Henschel *et al.* 2001; Murakami & Nakano 2002;

392Sato *et al.* 2016), a pattern usually attributed to predator numerical responses.

393The sequential shifts in top-down effects observed in our study have also been

394suggested in other studies of food-web dynamics following *in situ* resource pulses

395(Ostfeld & Keesing 2000; Yang *et al.* 2008, 2010). For example, acorn masting

396initiated a sequential shift in the top-down effects of raptors on thrushes in eastern

397North American forests (Schmidt & Ostfeld 2003, 2008; Schmidt *et al.* 2008).

398Sequential shifts between weakened and strengthened top-down control may also

399occur after pulses of rainfall in arid and semi-arid systems (e.g., Jaksic *et al.* 1997;

400Letnic & Dickman 2010; Greenville *et al.* 2014) and when enhanced resource

401availability accompanies food-web reassembly after disturbance (Spiller *et al.*

4022018). These latter cases are similar to the pulsed subsidies we studied as they are

403also donor controlled.

404Unlike the other response variables, web spiders tended to experience weaker,

405rather than stronger, top-down lizard effects beyond the first year of the

406experiment. We suggest that long-term increases in the abundance of invertebrate

407predators (e.g., wasps) in seaweed-addition treatments may have reduced web

408spider abundance on no-lizard islands, weakening the lizard effect.

409*How does the magnitude of pulsed subsidies influence top-down effects?*

410The influence of pulsed subsidy magnitude on lizard effects was most apparent in

411the short-term, when large seaweed inputs were associated with a more

412pronounced weakening of lizard effects on plant growth and salticid spider density,

413though both results were marginally significant (Fig. 2). These findings are

414consistent with stable isotope data from both the current study (Wright et al, in

415review) and previous observational studies (Piovia-Scott *et al.* 2013) indicating that

416the degree of diet shift can be associated with the magnitude of seaweed

417deposition. In the long term, the several large seaweed treatment, which featured

418three times more total seaweed than the other two seaweed treatments, was the

419only treatment associated with stronger lizard effects on buttonwood growth and

420leaf damage than the no-seaweed control (Fig. 2; significant for shoot growth,

421marginally significant for leaf damage). However, there was not strong evidence

422that the lizard effects in the several large treatment differed from those in the other

423two seaweed-addition treatments, though the trend is in that direction. Overall,

424these results suggest that increasing the magnitude of pulsed subsidies can

425increase the magnitude of shifts in top-down effects on plants without changing the

426temporal pattern of these effects (i.e., short-term weakening followed by long-term

427strengthening). In other words, pulsed subsidy magnitude was associated with

428quantitative, rather than qualitative, changes in top-down effects, consistent with

429our expectations.

430*How does the frequency of pulsed subsidies influence top-down effects?*

431The frequency of pulsed subsidies is likely to influence the strength of top-down

432effects by altering the relative importance of different response pathways (Takimoto

433*et al.* 2009). For example, increasing the frequency of seaweed pulses (without

434changing the cumulative amount of deposition) increased lizard effects on salticid

435spiders, which could be due to a less pronounced reduction in the lizard effect after

436the first seaweed addition in the several small treatment (see previous section).

437Notably, in our study there were no instances in which the second or third seaweed

438addition appeared to cause short-term weakening of lizard effects (Fig. 3),

439suggesting that any effects of subsequent seaweed additions associated with diet

440shifts were compensated for by other factors, such as numerical responses. Instead,

441the second seaweed addition led to increased lizard effects on leaf damage in both

442the several large and several small seaweed-addition treatments compared to both

443no-seaweed controls and the single large seaweed addition (Fig. 4). Lizard

444abundance was not higher in the several large and several small treatments than in

445the single large treatment (Wright *et al.*, in review), suggesting that the increased

446lizard effect associated with more frequent seaweed addition was not driven by a

447compounding lizard numerical response. Rather, it seems that the second seaweed

448addition was associated with increased leaf damage in the absence of lizards (Fig.

4495). This could be driven by herbivore numerical responses associated with increased

450plant nutritional quality resulting from rapid uptake of nutrients from the second

451seaweed addition (the fertilization effect). This hypothesis is bolstered by the fact

452that one of the most common herbivores in during this portion of the experiment,

453the pyralid moth *Dasyvesica nepomuca* Schaus, was particularly abundant on no-

454lizard islands after the second large seaweed addition (Piovia-Scott *et al.*,

455unpublished data). Overall, these results suggest that the frequency of pulsed

456subsidies may influence the temporal sequence of top-down effects on local

457resources through unexpected pathways, which may be influenced by the timing of

458pulses with respect to other environmental conditions (as in Sato *et al.* 2016).

459**Conclusions**

460The results of our field experiment show that a strong bottom-up perturbation can

461alter the strength of top-down effects in food webs in the sequential manner

462predicted by resource pulse theory (Ostfeld & Keesing 2000; Yang *et al.* 2008, 2010;

463Leroux & Loreau 2012). Bottom-up effects of detrital resource pulses were

464propagated upward through food webs via multiple pathways, each with distinct

465temporal signatures and effects on food-web dynamics. In the short-term, top-down

466effects of predators (including trophic cascades) were temporarily weakened,

467consistent with the effects of rapid predator diet shifts; this short-term weakening of

468cascading effects on plants was more pronounced with higher subsidy magnitude.

469Over longer periods of time, the coincidence of plant fertilization and high predator

470abundance created a 'window of opportunity' for strong cascading effects (Power *et*

471*al.* 1996, 2008; Piovia-Scott *et al.* 2017). Repeated pulses reinforced this

472phenomenon, suggesting that pulse frequency can play a key role in governing

473ecological responses to pulsed resource inputs. Future inquiries into the strength

474and importance of top-down control in food webs should anticipate the possibility of

475dramatic temporal variation in these effects and appreciate the role of past

476resource inputs, and the relative timescales of different bottom-up effects, in driving

477this variation.

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Figures

Figure 1. Hypothesized s**equential changes in the top-down effects of**

predators following a pulsed subsidy. Initially, we expect shifts in diet and/or

foraging behavior by resident predators to reduce their direct top-down effects on

lower trophic levels in the local environment (**a** - **c**). Over longer time scales, we

expect predator numerical responses and reduced availability of the pulsed

resource to increase the top-down effects of predators; plant fertilization may also

contribute to stronger top-down effects by increasing plant quality and growth rate,

increasing the intensity of herbivory in the absence of predators (**a**, **d**). In panels **b**,

c, and **d**, solid black arrows denote negative direct effects, dashed black arrows

denote positive indirect effects, and the dashed green arrow indicates

decomposition leading to plant fertilization. Arrow width is proportional to effect

size. The size of the lizard and the text labels of other trophic guilds is roughly

proportional to abundance (for animals) or growth (for plants). We do not include an

effect of spiders on plants as previous studies in this system found no evidence for

such an effect (Spiller & Schoener 1996).

Figure 2. Short-term and long-term shifts in top-down lizard effects in

response to pulsed seaweed subsidies. The y-axis shows short-term and long-

term changes in the effects of lizards on **a**) spiders and **b**) plants in different

seaweed treatments compared to no-seaweed controls (see Appendix S1 for

details). Negative values on the y-axis indicate a weaker lizard effect in the

seaweed treatment than in the no-seaweed control (i.e., lizard effects are less

negative for spiders, less positive for plants), positive values on the y-axis indicate a

stronger lizard effect in the seaweed treatment than in the no-seaweed control (i.e.,

lizard effects are more negative for spiders, more positive for plants). Asterisks

661indicate significant changes in the lizard effect compared to the no-seaweed control

662treatment. Estimated change in effect size and standard errors are shown; note that

663for salticid spiders effect sizes (and changes in effect sizes) were calculated as raw

664differences whereas for all other response variables effect sizes (and changes in

665effect sizes) are analogous to log response ratios (e.g., lizard effect = log[value with

666lizards/value without lizards]; see Appendix S1 for details). The sign of the lizard

667effect on leaf damage was reversed for plotting purposes so that the y-axis of the

668leaf damage plot is consistent with that of the shoot growth plot (a beneficial effect

669of lizards on plants corresponds with a positive effect on shoot growth and a

670negative effect on leaf damage).

671**Figure 3. Change in top-down lizard effects in response to different pulsed**

672**seaweed subsidy treatments.** The y-axis shows changes in the effects of lizards

673on **a**) spiders and **b**) plants in different seaweed treatments compared to no-

674seaweed controls during each sampling trip (see Appendix S1 for details). Negative

675values on the y-axis indicate a weaker lizard effect in the seaweed treatment than

676in the no-seaweed control (i.e., lizard effects are less negative for spiders, less

677positive for plants), positive values on the y-axis indicate a stronger lizard effect in

678the seaweed treatment than in the no-seaweed control (i.e., lizard effects are more

679negative for spiders, more positive for plants). Asterisks indicate significant changes

680in the lizard effect compared to the no-seaweed control treatment. Estimated

681change in effect size and standard errors are shown; note that for salticid spiders

682effect sizes (and changes in effect sizes) were calculated as raw differences

683whereas for all other response variables effect sizes (and changes in effect sizes)

684are analogous to log response ratios (e.g., lizard effect = log[value with

685lizards/value without lizards]; see Appendix S1 for details). The sign of the lizard

686effect on leaf damage was reversed for plotting purposes so that the y-axis of the

687leaf damage plot is consistent with that of the shoot growth plot (a beneficial effect

688of lizards on plants corresponds with a positive effect on shoot growth and a

689negative effect on leaf damage). Grey bars indicate seaweed-addition events; the

690red dashed line indicates the date of experimental lizard introductions.

691**Figure 4. Spider abundance on experimental islands.** The densities of **a**) web

692spiders and **b**) salticid spiders; means and standard errors are shown. Grey bars

693indicate seaweed-addition events; the red dashed line indicates the date of

694experimental lizard introductions. Note log scale on the y-axes. Web spider

695abundance was calculated as number per unit vegetated area; salticid abundance

696was calculated as number per bowl trap plus the number per tap sample. To avoid

697taking the log of zero, we added 0.01 to web spider abundance and 0.1 to salticid

698abundance prior to plotting; these numbers approximate the minimum non-zero

699measurement.

700**Figure 5. Plant growth and leaf damage on experimental islands. a**) shoot

701growth, and **b**) % leaf damage; means and standard errors are shown. Grey bars

702indicate seaweed-addition events; the red dashed line indicates the date of

703experimental lizard introductions. Note log scale on the y-axes.

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