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Uncoupling of omnivore-mediated positive and negative effects on periphyton mats

Received: 8 February 2002 / Accepted: 24 April 2003 / Published online: 27 May 2003
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Abstract The riverine grass shrimp (*Palaemonetes paludosus*) and eastern mosquitofish (*Gambusia holbrooki*) consume periphyton and small invertebrates, potentially affecting periphyton through negative effects (i.e., consumption) and/or positive effects such as nutrient regeneration, physical stimulation, and trophic cascades. We performed field experiments in the Everglades in which omnivores and periphyton were maintained in cages, with a fraction of the periphyton held in omnivore-exclusion bags that allowed passage of nutrients but prevented its consumption or physical disturbance. In some instances, periphyton growth rate increased with increasing omnivore biomass. Omnivores probably stimulated periphyton growth through nutrient regeneration, possibly subsidizing periphyton with nutrients derived from ingested animal prey. The net balance of omnivore-mediated negative and positive effects varied among experiments because of seasonal and spatial differences in periphyton characteristics. Consumption of periphyton mats might have been reduced by the arrangement of palatable algae (green algae and diatoms) within a matrix of unpalatable ones (CaCO₃-encrusting filamentous cyanobacteria). In a laboratory feeding experiment, mosquitofish consumed more green algae and diatoms in treatments with disrupted mat structure than in those with intact mats. No difference in diet was observed for shrimp. Our study underscores the complexity of consumer-periphyton interactions in which periphyton edibility affects herbivory and consumers influence periphyton through multiple routes that cannot be fully appreciated in experiments that only investigate net effects.

Keywords Florida Everglades · Grazing · Omnivory · Periphyton · Positive and negative effects

Introduction

It is commonly assumed that consumer-resource interactions are detrimental for the resources and beneficial for the consumers. However, consumers can positively affect resources through mechanisms that enhance their biomass and resources can negatively affect consumers through chemical or physical defenses that confer protection against herbivores (Huntly 1991; Steinman 1996). The net impact of consumers on primary producers will therefore depend on the relative magnitudes of deleterious and stimulatory effects, which in turn might be mediated by primary producer attributes such as defenses and edibility. In aquatic systems, two mechanisms by which consumers enhance primary production are nutrient regeneration and physical stimulation. Several studies in both pelagic and benthic systems have shown that consumer-mediated recycling or translocation of nutrients can alter the supply of resources to algae (Lamarra 1975; Porter 1976; Kitchell et al. 1979; Cuker 1983; Sterner 1986; Elser and Goldman 1990; McCormick and Stevenson 1991; Carpenter et al. 1992; McCormick 1994; Vanni 1996). Physical disturbance of algae and their microhabitat by aquatic consumers can enhance nutrient and light availability and potentially increase algal biomass. Examples of physical stimulation are the removal of overlying sediments (Power 1990; Pringle et al. 1993) and epiphytes (McCormick and Stevenson 1991; Kupferberg 1997), or disturbance of algal mat structure (McCormick 1994; Cattaneo and Mousseau 1995; Steinman 1996).

An interesting case is presented by omnivores because they also can: (1) decrease herbivorous grazers and thus increase algal biomass via trophic cascades; and (2) mobilize nutrients from ingested herbivores, providing a nutrient subsidy to primary producers that can even overcompensate for their herbivory (cf. de Mazancourt et al. 1998). In contrast, nutrient regeneration by herbivores

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can only return a fraction of nutrients removed from primary producers because of metabolic demands and assimilation. Despite these interesting potential effects, the role of omnivores in structuring communities remains poorly understood (Diehl 1993; Polis and Strong 1996).

Separating these different pathways is not a trivial matter, but can be partially accomplished by including nutrient-permeable, omnivore-exclusion bags inside experimental cages containing different densities of omnivores to uncouple some of these effects. A similar approach has been taken for grazer-algae systems by Sterner (1986) and Vanni and Layne (1997) [see Cuker (1983) and Elser and Goldman (1990) for alternative approaches]. Growth of algae in cages (i.e., exposed to omnivores and herbivorous grazers) should reveal the net effects of consumption, omnivore reduction of grazers through trophic cascades, increased nutrient availability, physical disturbance of algal mats, and any other effect arising from omnivory. In contrast, algal growth in nutrient-permeable bags (which exclude omnivores but may allow the passage of grazers) should reveal only the omnivore indirect effects that are spatially dispersed, such as nutrient regeneration, and the negative effects of grazer herbivory. Algae in the bags will not respond to stimulatory effects if they are very localized (e.g., stemming from physical disturbance of the algal matrix by the omnivores).

Interpretation of studies using omnivore-exclusion bags requires the assumption that omnivore-mediated nutrient effects are spatially dispersed, such that cages and bags experience the same nutrient environment. Consequently, the net effect of omnivores in cages could be negative, zero, or positive depending on the balance between negative (consumption) and positive effects (trophic cascades, nutrient regeneration, physical stimulation). The net effect of omnivores in bags could also be negative, zero, or positive depending on the balance between herbivory by grazers within bags (negative effect) and nutrient regeneration by omnivores in cages (positive effect). The value obtained after subtracting cage net effects from bag net effects (i.e., bag - cage) should represent all omnivore-mediated "localized effects" on algal growth. In other words, it should represent omnivore consumption corrected for any stimulation from localized processes (physical disturbance, trophic cascades) because spatially dispersed nutrient effects cancel out.

In the Florida Everglades, two omnivores, the riverine grass shrimp (*Palaemonetes paludosus* Gibbes) and the eastern mosquitofish (*Gambusia holbrooki* Girard), comprise the bulk of invertebrate and fish biomass (60% and 30% respectively; Turner et al. 1999). Previous dietary and isotope studies have shown that they feed on periphyton and small invertebrates (Hunt 1952; Beck and Cowell 1976; Loftus 2000). Periphyton biomass in the Everglades is unusually high despite being a very oligotrophic system, suggesting that periphyton is not under tight consumer control (Turner et al. 1999). However, no studies have yet addressed the effect of consumers on periphyton experimentally. Therefore, the purpose of this study was three-fold: (1) to determine the

net effects of these two omnivores on periphyton biomass in the Florida Everglades; (2) to uncouple omnivore-mediated localized effects including consumption from dispersed effects mostly affected by nutrient dynamics; and (3) to assess if the physical structure of periphyton mats protected the relatively more edible algae from being consumed. We hypothesize that the high periphyton biomass in the Everglades might be partially related to its edibility and mat structure (Geddes 1999).

Methods

Field experiments

We conducted three field experiments (which we call "early dry season", "wet season", and "late dry season") in Everglades National Park, Florida (Table 1). We used mesh cages to enclose omnivores with periphyton. Cages enclosed an area of 1 m², had 2 mm mesh on four sides and the bottom, and were open at the top. In the wet and late dry season experiments, we also placed an omnivore-exclusion bag (25 cm in diameter, 30 cm long) inside each cage (Table 1). The opening of the bags floated at the water surface and the bag hung into the water column without reaching the sediments. These bags were designed to exclude shrimp and fish, while permitting nutrients to pass through the bag mesh (~1.5 mm). We did not attempt to remove invertebrates in periphyton mats before adding them to cages or bags and, given our choice of mesh sizes, any invertebrates smaller than ~2 mm could move in and out of cages and bags freely from the surrounding water.

We crossed three densities (0, ambient, and 3× ambient) of mosquitofish and shrimp, resulting in nine different treatments that included a control with no fish or shrimp (Table 1). Ambient densities were based on data from ongoing monitoring studies of the southern Everglades that include our experimental sites (Loftus and Eklund 1994; Trexler et al. 2001). For mosquitofish, the average ambient density across ten sampling events between July 1996 and April 1998 was 3 individuals m⁻², with a range of 1 to 4 (J.C. Trexler, unpublished data). For shrimp, the average ambient density was 18 individuals m⁻², ranging from 4 to 42 (J.C. Trexler, unpublished data). Omnivore survival in our experiments was independent of treatment and generally high (>80%), except for shrimp in the wet season experiment (46%), where oxygen stress before being introduced to cages might have been responsible for their mortality (Geddes 1999). There was also a small amount of recruitment of shrimp and mosquitofish to our experimental cages. Overall, however, the gradient of omnivore density and biomass was maintained.

To estimate omnivore biomass and growth rates, we counted and measured omnivores at the beginning and end of the experiments. For mosquitofish, we used length-wet biomass regressions (Kushlan et al. 1986). For shrimp, we first converted carapace length (CL) into total length (TL) [$TL(mm) = 2.218 + 2.11 \times CL(mm)$, $n=100$, $R^2=0.95$; Eklund and Loftus unpublished data], and then converted TL into wet mass using the relationship given in Kushlan et al. (1986). Even though shrimp and mosquitofish experienced negative density-dependent effects on their growth at high densities (Geddes 1999), growth rates at ambient densities were comparable to estimates for similarly aged animals in the field (Taylor et al. 2001), suggesting no cage artifacts on omnivore growth.

At the outset of each experiment, we added 2,300–2,400 g wet-mass of periphyton floating mats to each cage and 300 g to each bag. The combined amounts of periphyton in cages and bags were within the natural biomass range of periphyton in the field (J.C. Trexler, unpublished data). We sampled periphyton from each cage and bag at the beginning and end of the experiments to estimate wet-mass, chlorophyll *a* (spectrophotometer determination), AFDM, and periphyton phosphorus (P) content following standard methods

Table 1 Summary of field experiments conducted during this study

	Early dry season	Wet season	Late dry season
Location	Taylor Slough	Taylor Slough	Shark River Slough
Date of experiment	28 February–18 March 1998	10 August–28 August 1998	18 March–12 April 1999
Duration of experiment	8 days	18 days	25 days
Experiment season	Early dry	Wet	Late dry
Omnivore-exclusion bag used?	No	Yes	Yes
Dependent variable analyzed:			
Wet-mass growth rate	Yes	Yes	Yes
Chlorophyll <i>a</i> growth rate	Yes	Yes	Yes
AFDM growth rate	Yes	Yes	Yes
Periphyton P growth rate	No	Yes	Yes
Initial shrimp density in cages	0, 20, 60	0, 20, 60	0, 20, 60
Initial fish density in cages	0, 3, 9	0, 3, 9	0, 5, 15 ^a
Replicates per treatment	3	3	6
Final sample size ^b	24	27	53
Blocks	3	3	2

^a Mosquitofish densities were raised from 0, 3, and 9 to 0, 5, and 15 to better reflect natural densities at this experimental site. Though field densities of shrimp were also greater at this site, we used the same densities as in previous experiments because of logistic constraints in handling more shrimp. Note that analyses of omnivore effects were conducted on the combined biomass of fish and shrimp and not on their density (see Methods)

^b Due to weather conditions that overturned some cages or failed sample preservation, some replicates are missing

(Eaton et al. 1995; Table 1). We measured periphyton P content because P is the limiting nutrient for periphyton growth in the Everglades, where total P values are typically less than 10 $\mu\text{g l}^{-1}$ (McCormick and O'Dell 1996; McCormick et al. 1996). Chlorophyll *a* measures the biomass of photosynthetic organisms in periphyton mats, and AFDM measures all organic biomass (including algae, invertebrates, bacteria, fungi, etc.). Wet-mass measures the combined wet biomass of photosynthetic algae, organic matter, and inorganic matter. Periphyton P reflects nutrient content of all organisms as well as P adsorbed to organic and inorganic matter.

To facilitate comparisons across experiments and variables, we calculated instantaneous growth rates for all dependent variables (periphyton wet-mass, chlorophyll *a*, AFDM, and P content) as $\ln(N_f/N_0)/t$, where N_f is the final periphyton biomass at the end of the experiment, N_0 is the initial periphyton biomass at the beginning of the experiment, and t is the duration of the experiment in days (Table 1). In the wet season experiment, we did not have initial values (N_0) for periphyton P content. Therefore, to keep analyses and interpretation of all variables as consistent as possible, we assumed that $N_0=c$, a constant, arbitrary value, and calculated instantaneous growth rate of P content as $\ln(N_f/c)/t$ for cages and bags. The arbitrary choice of c ($c_{\text{cage}}=3439.51 \mu\text{g P/cage}$; $c_{\text{bag}}=786.58 \mu\text{g P/bag}$) ignores real variation in N_0 ; however, this periphyton P growth rate approximation should nevertheless be proportional to the actual instantaneous growth rate.

To account for spatial patchiness, experiments were established with two or three blocks (Table 1). We assumed no interaction between blocks and other factors in the models (Newman et al. 1997), and interpreted block effects to reflect spatial differences in periphyton dynamics.

Cage and bag artifacts on periphyton growth might bias our estimates of omnivore effects. As a test for artifacts, we performed two analyses. First, we used paired *t*-tests to compare periphyton growth rates in cages and bags of control treatments (no omnivores present). All test results were non-significant but they had limited power due to small sample sizes ($n=3$). Therefore, we performed analysis of covariance (ANCOVA) to compare estimates of intercepts from regressions of algal growth on omnivore biomass (see below).

Initial factorial ANOVA testing for the separate effects of fish and shrimp density and their interaction on periphyton growth suggested that their effects were additive. In addition, omnivores experienced negative density-dependent growth (Geddes 1999). Our experiments also used widely different densities for each consumer, thus confounding taxon identity and abundance

(Feminella and Hawkins 1995). Consequently, we used the combined biomass of mosquitofish and shrimp as the independent variable in all statistical analyses.

To examine the net effect of increasing omnivore biomass and the effects of nutrient regeneration on periphyton growth rate, we performed ANCOVA on each dependent variable for the wet and late dry season experiments. The model included a block factor, a compartment factor (cage or bag), the covariate (omnivore biomass), and the interaction between compartment and the covariate. Negative regression coefficients of individual regression lines indicated net negative effects on periphyton growth rate, whereas positive regression coefficients indicated net positive effects (i.e., enhancement of growth rate).

In an effort to uncouple omnivore-mediated localized effects (including consumption) from dispersed effects mostly affected by nutrient dynamics, we subtracted periphyton growth rate in cages from periphyton growth rate in bags (where omnivores had no access to periphyton), and regressed these values on total omnivore biomass. We expected localized effects of omnivores on periphyton to increase with increasing omnivore biomass (positive slope) because we assumed increased biomass of omnivores would lead to higher nutrient regeneration and increased consumption (i.e., bag net effects > cage net effects). The model included a block factor and an omnivore biomass factor.

Laboratory experiment

In July 1998, we conducted a laboratory experiment to determine the effects of periphyton mat structure on the edibility of and/or accessibility to particular algae. Omnivores were assigned to one of two possible treatments: "intact mat," which received a periphyton mat that remained as collected from the field, or "disrupted mat," which received a periphyton mat that was shaken in a closed container to destroy mat structure. We collected mats from the same location and standardized their size (52.5 cm²) before assigning them to treatments.

Treatments were randomly assigned to either shrimp or mosquitofish in plastic tanks with 1,300 ml water. Several fish and shrimp were starved for 3 days to standardize their level of hunger, and we analyzed gut contents of three randomly picked specimens of each taxon to ensure that their stomachs had indeed been cleared. Once the mats (disrupted or intact) had been placed in tanks, we added three mosquitofish or three shrimp per tank

according to treatment, with six replicates per treatment per omnivore type, for a total of 24 tanks.

The experiment ran for 3 days, after which we collected the omnivores between 10 and 12 a.m., sacrificed them using the anesthetic MS-222, and preserved them in 10% formalin. Using a compound microscope, we enumerated algal stomach contents as numbers of biological units (i.e., cells for unicellular taxa, 10- μ m segments for filamentous taxa, and colonies for colonial taxa; Eaton et al. 1995) and invertebrates.

Stomach contents of the three specimens (mosquitofish or shrimp) were averaged in each tank. Algal taxa were pooled into four taxonomic groups (filamentous cyanobacteria, coccoid cyanobacteria, green algae, and diatoms) and we combined all invertebrates (ciliates, rotifers, ostracods, copepods, chydorids, cladocerans, mites, chironomids, nematodes, insect parts) into a single variable, yielding a total of five diet categories. We square-root transformed the data to fulfill parametric assumptions, and analyzed the data separately for fish and shrimp using multivariate analysis of variance (MANOVA).

Results

Field experiments

Early dry season experiment

Mean wet-mass growth rate in control cages was negative, consistent with natural dry-season dynamics (mean = $-0.0396 \text{ g day}^{-1}$; 95% confidence limits = -0.0726 and -0.0065). However, chlorophyll *a* and AFDM exhibited little change. Mean chlorophyll *a* growth rate was $-0.0030 \text{ } \mu\text{g day}^{-1}$ (95% confidence limits = -0.0621 and 0.0017) and $-0.0181 \text{ g day}^{-1}$ for mean AFDM growth rate (95% confidence limits = -0.0367 and 0.0005).

The presence of fish and shrimp in cages slowed the decline for wet-mass growth rate and enhanced chlorophyll *a* and AFDM growth rates, providing no evidence of negative effects such as consumption (Fig. 1). Omnivores enhanced periphyton growth rate as wet-mass ($F_{1,20}=13.82$, $P<0.01$; Fig. 1a) and chlorophyll *a* ($F_{1,20}=9.24$, $P<0.01$; Fig. 1b). At the highest biomass of omnivores, the absolute change from controls in wet-mass growth rate was increased by 0.023 day^{-1} and by 0.034 day^{-1} for chlorophyll *a*. Although not significant, there was a similar increasing trend for AFDM growth rate with increasing omnivore biomass ($F_{1,20}=2.60$, $P=0.12$; Fig. 1c). Block was significant for periphyton wet-mass ($F_{2,20}=4.91$, $P=0.02$) and chlorophyll *a* ($F_{2,20}=3.43$, $P=0.05$), and marginally significant for AFDM ($F_{2,20}=3.21$, $P=0.06$).

Wet season experiment

Analyses of covariance indicated that there was homogeneity in slopes of cages and bags for all periphyton growth rate measures as revealed by the lack of a significant interaction term between the covariate (omnivore biomass) and compartment (bag or cage) (Table 2A–D). In addition, there was a significant effect of the compartment (bag or cage) for periphyton wet-mass and AFDM growth rate (Table 2A, C), with bag least-squares means always

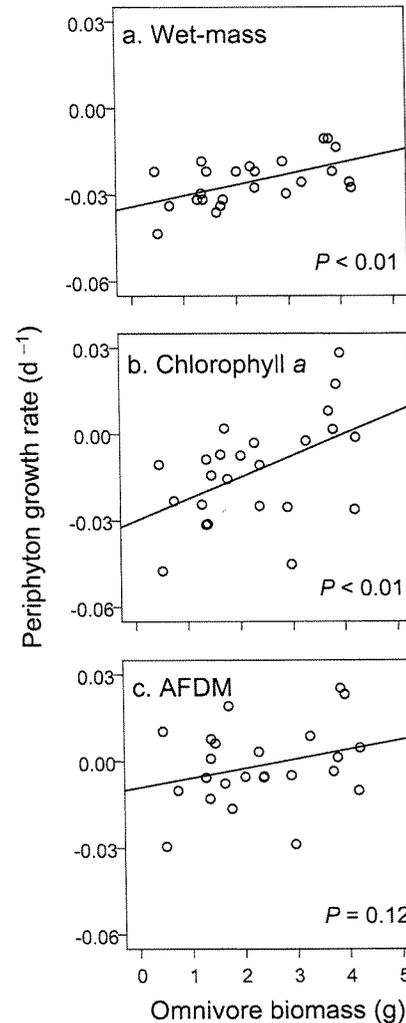


Fig. 1 Net effects of omnivore biomass on periphyton growth rates for the early dry season experiment

larger than cage least-squares means. This result suggests that bag and cage regression lines had different elevations (y-intercepts). Block was significant for all periphyton growth rate measures (wet-mass, chlorophyll *a*, AFDM, and P content) (Table 2A–D).

Increasing omnivore biomass had net positive effects for several periphyton growth rate measures. Analyses of covariance revealed that omnivore biomass had a significant positive effect on cage wet-mass and cage chlorophyll *a* growth rate (Fig. 2a, b; Table 2A, B), a marginally significant positive effect on bag chlorophyll *a* and cage AFDM (Fig. 2b, c; Table 2B, C), and no effect on periphyton P content (Fig. 2d; Table 2D).

Increasing omnivore biomass did not affect their localized effects on periphyton. Regression analyses of the difference between bag and cage periphyton growth rates versus total omnivore biomass exhibited slopes not significantly different from zero for all periphyton growth rate measures (Fig. 3a–d; Table 3A–D). Block was

Table 2 ANCOVA results for the wet and late dry season experiments. Growth rate was analyzed for each dependent variable

Source	df	MS	F	P
Wet season experiment				
A) Periphyton wet-mass; $R^2=0.44$				
Block	2	0.0003	4.8618	0.0120
Omnivore biomass	1	0.0003	4.7051	0.0351
Compartment (cage or bag)	1	0.0090	14.2013	0.0005
Omnivore biomass×compartment	1	0.0001	1.5405	0.2206
Error	48	0.0001		
B) Chlorophyll <i>a</i> ; $R^2=0.38$				
Block	2	0.0026	10.2701	0.0002
Omnivore biomass	1	0.0020	7.6736	0.0080
Compartment (cage or bag)	1	0.0007	2.8090	0.1002
Omnivore biomass×compartment	1	0.0001	0.3116	0.5793
Error	48	0.0003		
C) AFDM; $R^2=0.41$				
Block	2	0.0004	3.6262	0.0342
Omnivore biomass	1	0.0004	3.6512	0.0620
Compartment (cage or bag)	1	0.0015	12.2141	0.0010
Omnivore biomass×compartment	1	0.0001	1.0621	0.3079
Error	48	0.0001		
D) Periphyton P content; $R^2=0.48$				
Block	2	0.0015	22.5701	<0.0001
Omnivore biomass	1	0.0002	2.6909	0.1075
Compartment (cage or bag)	1	0.0001	0.0699	0.7926
Omnivore biomass×compartment	1	0.0001	0.0791	0.7797
Error	48	0.0001		
Late dry season experiment				
E) Periphyton wet-mass; $R^2=0.37$				
Block	1	0.0001	2.6154	0.1090
Omnivore biomass	1	0.0001	0.8131	0.3693
Compartment (cage or bag)	1	0.0001	1.9163	0.1693
Omnivore biomass×compartment	1	0.0001	6.2043	0.0144
Error	101	0.0001		
F) Chlorophyll <i>a</i> ; $R^2=0.06$				
Block	1	0.0002	1.7128	0.1936
Omnivore biomass	1	0.0001	0.0120	0.9130
Compartment (cage or bag)	1	0.0001	0.1152	0.7350
Omnivore biomass×compartment	1	0.0002	1.8607	0.1756
Error	101	0.0113		
G) AFDM; $R^2=0.14$				
Block	1	0.0001	0.0261	0.8721
Omnivore biomass	1	0.0001	1.2738	0.2617
Compartment (cage or bag)	1	0.0001	0.0890	0.7660
Omnivore biomass×compartment	1	0.0002	5.0080	0.0274
Error	101	0.0001		
H) Periphyton P content; $R^2=0.32$				
Block	1	0.0135	45.4470	<0.0001
Omnivore biomass	1	0.0003	0.8973	0.3458
Compartment (cage or bag)	1	0.0005	1.6591	0.2007
Omnivore biomass×compartment	1	0.0003	1.0761	0.3021
Error	100	0.0003		

significant for all variables analyzed (wet-mass, chlorophyll *a*, AFDM), except periphyton P (Table 3A–D).

Late dry season experiment

Analysis of covariance revealed that there was heterogeneity in slopes of cages and bags for periphyton wet-mass

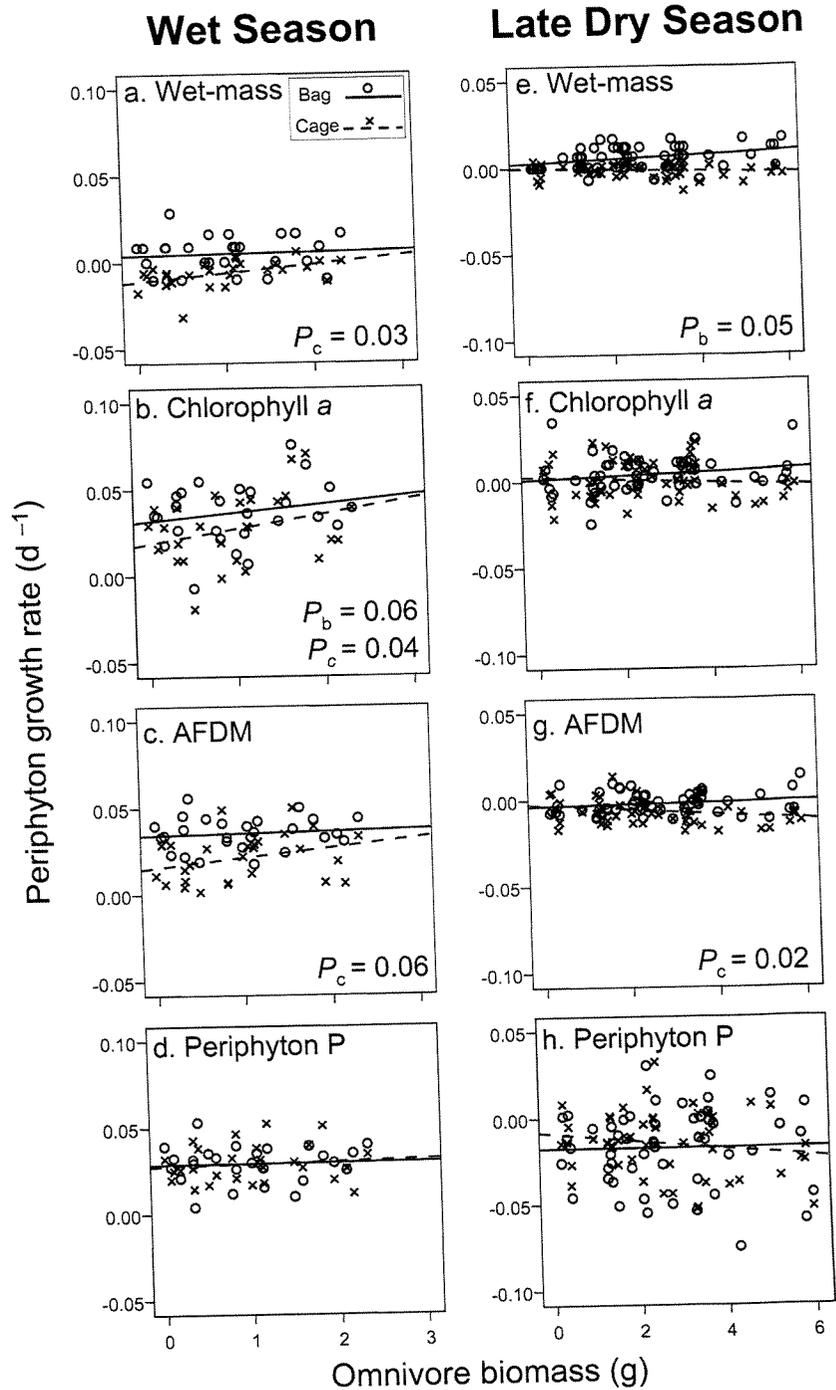
Table 3 Results for regression analyses on the localized effects of omnivore biomass on periphyton growth rate for the wet and late dry season experiments. The difference between bag and cage periphyton growth rates was analyzed for each dependent variable

Source	df	MS	F	P
Wet season experiment				
A) Periphyton wet-mass; $R^2=0.41$				
Block	2	0.0006	6.6534	0.0053
Omnivore biomass	1	0.0001	0.8209	0.3743
Error	23	0.0001		
B) Chlorophyll <i>a</i> ; $R^2=0.53$				
Block	2	0.0017	12.2096	0.0002
Omnivore biomass	1	0.0002	1.3075	0.2646
Error	23	0.0001		
C) AFDM; $R^2=0.59$				
Block	2	0.0015	15.0343	<0.0001
Omnivore biomass	1	0.0002	2.0616	0.1645
Error	23	0.0001		
D) Periphyton P; $R^2=0.09$				
Block	2	0.0001	1.1041	0.3485
Omnivore biomass	1	0.0001	0.2742	0.6055
Error	23	0.0001		
Late dry season experiment				
E) Periphyton wet-mass; $R^2=0.14$				
Block	1	0.0001	0.3731	0.5441
Omnivore biomass	1	0.0003	8.0431	0.0066
Error	50	0.0001		
F) Chlorophyll <i>a</i> ; $R^2=0.09$				
Block	1	0.0001	1.0223	0.3168
Omnivore biomass	1	0.0004	4.0610	0.0493
Error	50	0.0001		
G) AFDM; $R^2=0.27$				
Block	1	0.0005	9.4924	0.0034
Omnivore biomass	1	0.0005	9.3359	0.0036
Error	50	0.0001		
H) Periphyton P; $R^2=0.04$				
Block	1	0.0001	0.1183	0.7324
Omnivore biomass	1	0.0006	1.7978	0.1862
Error	49	0.0004		

and AFDM, as indicated by significant interaction terms between compartment (bag or cage) and the covariate (omnivore biomass) (Table 2E, G). Slopes for bag and cage chlorophyll *a* and periphyton P content were homogeneous as indicated by non-significant interaction terms between the compartment (bag or cage) and omnivore biomass (Table 2F, H). There were no significant compartment effects for any of the dependent variables (Table 2E–H), suggesting that cage and bag regression lines had equal elevations (*y*-intercepts). Block was significant only for P content (Table 2H).

Because of significant interaction terms between compartment (bag or cage) and the covariate (omnivore biomass) for periphyton wet-mass and AFDM growth rates, we contrasted effects of omnivore biomass separately for cages and bags for these dependent variables. Increasing omnivore biomass had both positive and negative net effects on periphyton growth rate. Omnivore biomass had a significant positive effect on bag wet-mass

Fig. 2 Net effects of omnivore biomass on cage and bag periphyton growth rates for the wet and late dry season experiments. P_c and P_b values denote significant regressions for cages and bags, respectively. Only significant regressions are reported

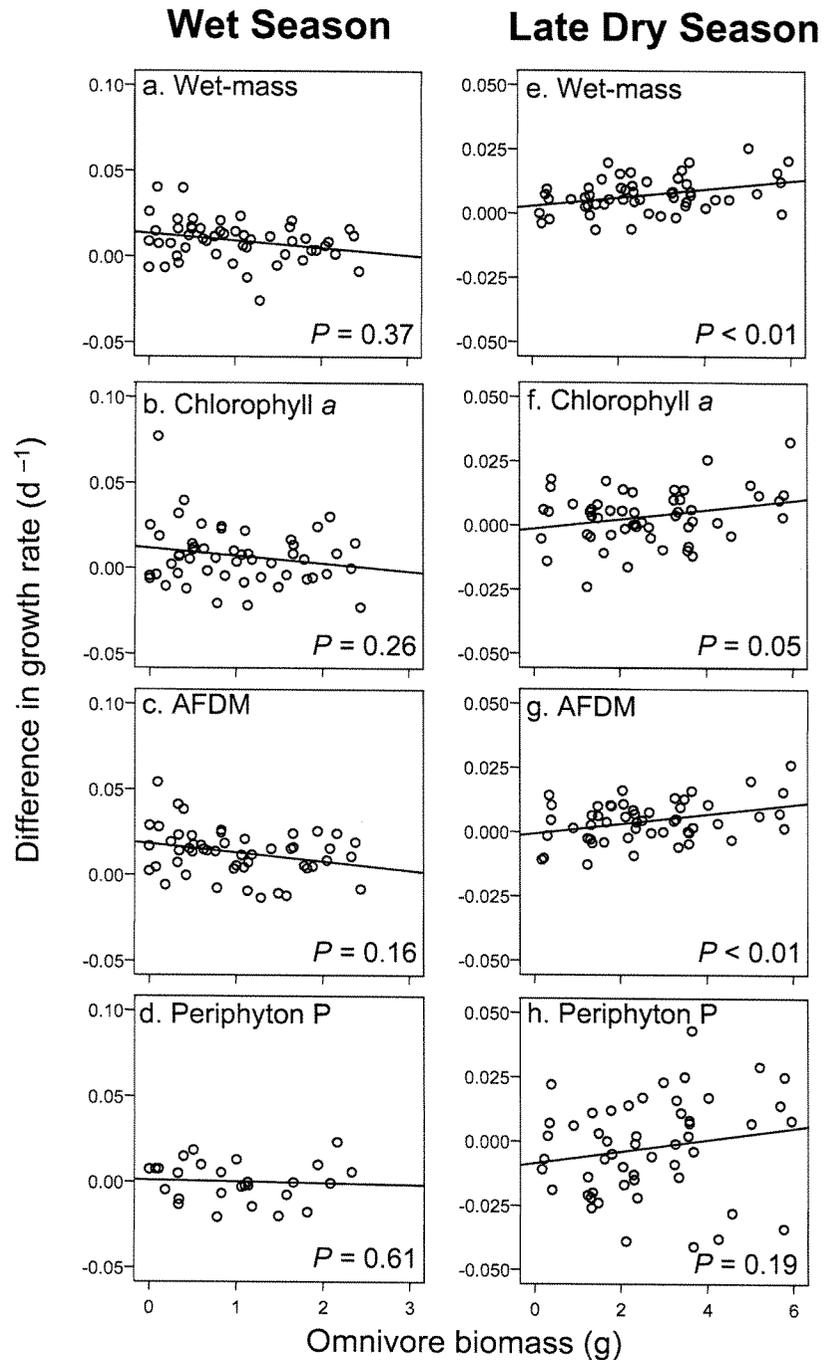


(Fig. 2e), a significant negative effect on cage AFDM (Fig. 2g), and no effect on chlorophyll *a* or periphyton P content (Fig. 2f, h).

Localized omnivore effects in cages were strong, as indicated by a significant positive slope in regression analyses of the difference between bag and cage periphyton growth rates versus total omnivore biomass. This result was observed for all measures of periphyton growth rate (wet-mass, chlorophyll *a*, and AFDM), except for

periphyton P content (Fig. 3e-h; Table 3E-H). At the highest omnivore biomass, the mean absolute increase of localized effects from controls was 0.0111 day⁻¹ for wet-mass, 0.0101 day⁻¹ for chlorophyll *a*, and 0.0118 day⁻¹ for AFDM. Block was significant only for AFDM growth rate (Table 3G).

Fig. 3 Localized effects of increasing omnivore biomass on periphyton growth rate for the wet and late dry season experiments. Localized effects were calculated as the difference between bag and cage periphyton growth rate and represent consumption corrected for any localized stimulation occurring in cages (see Introduction)



Laboratory experiment

Periphyton mat structure affected the diet of mosquitofish, but did not appear to affect the diet of shrimp. Mat treatment (disrupted versus intact) significantly affected mosquitofish consumption of all prey categories (Wilk's lambda=0.11, $P < 0.01$), but it had no significant effect on shrimp (Wilk's lambda=0.67, $P = 0.53$). Mosquitofish consumed relatively more edible algal taxa in disrupted-mat treatments compared to intact mats. The average

number of diatoms and green algae found in mosquitofish gut contents were higher in the disrupted-mat treatment than in the intact-mat treatment (Table 4). These differences were statistically significant (diatoms: $F_{1,10} = 32.43$, $P < 0.01$; green algae: $F_{1,10} = 34.38$, $P < 0.01$), explaining approximately 76% and 77% of the variance, respectively.

Table 4 Mean stomach contents of mosquitofish and shrimp (number of cells or animals per stomach) from the laboratory experiment (untransformed data). Standard deviations across tanks ($n=6$) are listed in parentheses. *I* intact-mat treatment, *D* disrupted-mat treatment, *Fil. cyanob.* filamentous cyanobacteria, *Cocc. cyanob.* coccoid cyanobacteria

Grazer	Treatment	Fil. cyanob.	Cocc. cyanob.	Green algae	Diatoms	Invertebrates
Fish	I	716.47 (760.13)	1.72 (2.27)	4.28 (2.39)	0.78 (0.54)	18.39 (16.17)
	D	632.18 (763.76)	3.61 (2.20)	45.22 (25.10)	10.72 (5.81)	6.00 (7.50)
Shrimp	I	479.27 (643.92)	1.06 (1.72)	3.45 (5.42)	0 (0)	0.39 (0.68)
	D	634.36 (1258.57)	0.72 (1.16)	40.00 (73.09)	0 (0)	0 (0)

Discussion

Omnivore effects on periphyton

Our experiments revealed that omnivores had net negative effects on periphyton growth rate as seen in the late dry season experiment (Fig. 2g; Table 5). However, in all three field experiments there were instances in which net positive consumer effects were also observed, providing evidence for stimulation of periphyton growth (Table 5). The net effect of omnivores, both consumptive and stimulatory, varied among experiments, probably as a result of seasonal dynamics and spatial patterns of periphyton growth. Spatial heterogeneity of periphyton in our experiments was evidenced by significant block factors in all statistical models for the three field experiments. Below, we propose potential mechanisms that could explain our results according to our conceptual framework.

The early dry season experiment provided strong evidence of net periphyton enhancement by omnivores (Fig. 1). This result could have been brought about by nutrient-mediated or physical stimulation by omnivores and thus prompted us to use nutrient-permeable, omnivore-exclusion bags in subsequent experiments. Hillebrand and Kahlert (2001) found that periphyton nutrient content increased in the presence of grazers but their experimental design could not reveal whether the putative mechanism was physical stimulation or nutrient regeneration. Gresens (1995) documented a lack of grazer negative effects on periphyton AFDM, possibly as a result of grazer-mediated stimulation. The inability to isolate the mechanism potentially responsible for these interesting experimental results underscores the benefits of including treatments that allow at least partial uncoupling of effects that could otherwise remain masked if only net effects are assessed. Note that our design cannot separate all effects of omnivores on periphyton. The bag manipulation, however, does allow us to examine the role of omnivores on some aspects of nutrient dynamics.

We did not find evidence of negative or positive localized effects in the wet season experiment. Regression slopes of bag net effects minus cage net effects versus increasing omnivore biomass were not significantly different from zero (Fig. 3a–d). This result suggests that bag and cage effects were completely and exactly counterbalanced (bag effects–cage effects=0) across

Table 5 Summary of results for the three field experiments. Entries denote sign (and significance) of the coefficient for the regression of periphyton growth rates versus increasing omnivore biomass. N/A Not applicable

	Cage net effects	Bag net effects	Bag–cage (localized effects)
Early dry season			
Wet-mass	Positive*	N/A	N/A
Chlorophylla	Positive*	N/A	N/A
AFDM	Positive	N/A	N/A
Wet season			
Wet-mass	Positive*	Positive	Negative
Chlorophylla	Positive*	Positive ^{ms}	Negative
AFDM	Positive ^{ms}	Positive	Negative
Periphyton P	Positive	Positive	Negative
Late dry season			
Wet-mass	Negative	Positive*	Positive*
Chlorophylla	Negative	Positive	Positive*
AFDM	Negative*	Positive	Positive*
Periphyton P	Negative	Positive	Positive

* Significant at $P \leq 0.05$

^{ms} marginally significant ($0.05 < P < 0.10$)

increasing omnivore biomass, an outcome that seems unlikely. Caution should be taken when interpreting results about localized effects in this experiment because artifacts might have been responsible for such a pattern. Cages and bags had significantly different periphyton biomass as evidenced by significant compartment effects in ANCOVA (Table 2A, C), a highly undesirable outcome that weakens any attempt to explain observed patterns from analysis involving the difference of bag and cage values. With this in mind, however, we believe there is evidence that supports omnivore-mediated stimulation in the wet season experiment. The significant increase of cage periphyton wet-mass (Fig. 2a) and cage chlorophyll *a* (Fig. 2b), and the marginally significant increase of bag chlorophyll *a* (Fig. 2b) and cage AFDM (Fig. 2c) with increased omnivore biomass suggested enhancement of periphyton growth. These results should be robust to artifacts because they report cage and bag effects separately and independently (i.e., not their difference as in localized effects). Given that bag and cages had homogeneous slopes for all periphyton growth rate measures (Table 2A–D), suggesting that cage and bag responded identically to omnivore biomass, we believe

nutrient regeneration was an important positive effect of omnivores on periphyton mats of this experiment.

Localized effects in the late dry season experiment appeared to be strong. Regression slopes of localized effects (bag net effects–cage net effects) versus increasing omnivore biomass were significantly positive for all periphyton measures except P (Fig. 3e–h). A significantly positive slope indicated that the difference between bag and cage effects was increasingly greater with increasing omnivore biomass. Plausible explanations include: (1) increased nutrient regeneration with increased omnivore biomass (i.e., net positive bag effects); (2) increased consumption with increased omnivore biomass (i.e., net negative cage effects); and (3) both (1) and (2) occurred simultaneously. Because the net effect of increasing omnivore biomass was negative for cage AFDM (Fig. 2g) but positive for bag periphyton wet-mass (Fig. 2e; Table 5 also shows that all dependent variables responded in a similar fashion), we believe the net negative effects in cages incorporate some stimulation from nutrient regeneration by omnivores (but not enough to yield net positive effects as documented in the early dry season experiment). In this experiment, naturally senescing periphyton mats may have had less capacity to respond to omnivore-mediated stimulation than mats from the early dry season experiment (Fig. 1), conducted in the same season of the preceding year but approximately a month earlier and in a different region of the Everglades (Table 1).

We predicted an increase in bag periphyton P content if nutrient regeneration by omnivores was likely to have an effect on periphyton mats (cf. Hillebrand and Kahlert 2001). Our results did not show evidence for increased bag periphyton P content in any experiment. Though not significant, the effect of increasing omnivore biomass on bag periphyton P content was positive for the wet and late dry season experiments (Table 5), agreeing with nutrient-mediated omnivore stimulation. This result, taken together with positive slopes for all periphyton growth rate measures in bags in all experiments (Table 5), suggests that omnivores probably had positive effects on periphyton growth rate through nutrient-mediated stimulation. Macroinvertebrates and fish may play an important role in nutrient cycling in the oligotrophic environment of the Everglades by translocating nutrients within the food web, as has also been shown for other systems (Lamarra 1975; Brabrand et al. 1990; Vanni and Findlay 1990; Carpenter et al. 1992; Matveev et al. 1994; Vanni 1996; Vanni and Layne 1997; Schaus and Vanni 2000).

The role of omnivores in nutrient translocation within food webs remains relatively unappreciated (but see Drenner et al. 1996; Vanni 1996; Schaus and Vanni 2000). Theoretical models of direct and indirect effects of grazers on primary producers suggest that primary production increases in situations where grazers facilitate cycling of a limiting nutrient (DeAngelis 1992; Loreau 1995), with surplus plant production generated by grazer stimulation absorbed by the grazer trophic level. Consequently, plant biomass could only increase if grazers provide a new source of nutrients (i.e., subsidies) to

primary producers (de Mazancourt et al. 1998). An example of the latter phenomenon has been documented in lakes, in which fish feed on the benthic and littoral zones but later excrete their nutrients in the pelagic zone, thus subsidizing planktonic algae (Schindler et al. 1996; Schindler and Scheuerell 2002). Similar evidence has been observed in marine systems (e.g., Meyer et al. 1983; Krause and Bray 1994; Bouchard and Bjorndal 2000) and estuaries (Deegan 1993). In addition to consuming herbivorous grazers, thus releasing primary producers from some grazing via trophic cascades, omnivores could also yield increased plant biomass through translocation of nutrients from animal prey. This latter, less appreciated pathway than trophic cascades could therefore subsidize primary producers. Interestingly enough, however, preliminary models suggest that these subsidizing effects might only be transient and depend on the ability of omnivores to recycle nutrients sufficiently more efficiently than herbivorous invertebrates (C. de Mazancourt, personal communication). Further theoretical exercises combined with experiments specifically designed to test model predictions should enhance our understanding of the effect of omnivores as potential subsidizers of primary producers in food webs.

Though literature reviews suggest that positive effects of consumers on periphyton are “rare” cases (Cuker 1983; Feminella and Hawkins 1995; Steinman 1996), we believe certain ecosystem attributes deserve closer inspection because they have, according to theory, increased likelihood of yielding positive consumer effects on primary producers. Such attributes include intense oligotrophy, as in our system (but see Hudson et al. 1999), consumers that have the potential of introducing limiting nutrients from outside sources (e.g., Schindler et al. 1996), and high incidence of omnivory (Drenner et al. 1996; Vanni 1996; Schaus and Vanni 2000).

Consumer-periphyton dynamics in the Everglades: periphyton edibility

In our experiments, periphyton consumption was sometimes coupled with processes that stimulated periphyton growth rate. However, the net effect of omnivores on periphyton might have also been affected by primary producer attributes such as defenses and edibility. Chemical, structural, and physical defenses that protect plants against herbivores can result in negative effects on consumers and decreased herbivory (Porter 1977; Leibold 1989; Steinman 1996). We believe the structure and characteristics of Everglades periphyton mats may also help explain the unusual abundance of periphyton because of their potential negative effect on consumers.

Everglades periphyton mats hold together by CaCO₃-encrusting cyanobacteria and filamentous macrophytes (Merz 1992; Geddes 1999). Algal CaCO₃ acts as a grazer deterrent in marine systems (Pennings and Paul 1992; Hay et al. 1994), and we suggest that it may also discourage algal consumption in the freshwater Ever-

glades. Microscopic observations of paraffin-embedded periphyton mats revealed that live cells of diatoms and green algae can reside inside the calcified matrix of filamentous cyanobacteria (Geddes 1999). This structure may limit edibility of and/or accessibility to some algal taxa, consistent with patterns derived from associational resistance, an association of palatable species with unpalatable ones that reduces losses from herbivory (Atsatt and O'Dowd 1976). Associational resistance has been documented in terrestrial (e.g., McNaughton 1978) and marine systems (Pfister and Hay 1988; Wahl and Hay 1995) but the evidence for it in freshwater systems is sparse (Huntly 1991).

Our laboratory experiment demonstrated that the structure and distribution of algal taxa in periphyton mats influenced feeding by mosquitofish, but not by shrimp. The relative success of consumers feeding on periphyton is related to the suitability of their mouthparts and appendages to the structure of the periphyton assemblage (Steinman 1996; Jones et al. 1998). Shrimp feeding appendages may have allowed access to the palatable algae inside the mat, freeing them from structure-imposed feeding constraints. Green algae and diatoms, the two taxa consumed in greater amounts by mosquitofish in the laboratory experiment, are in general more palatable than cyanobacteria (Porter 1977; Lamberti 1996). Thus, the more palatable species might have been less vulnerable to herbivory by mosquitofish by being embedded inside the mat formed by less-palatable, calcified filamentous cyanobacteria, consistent with associational resistance. Jones et al. (1998) suggested that once periphyton mats become older and start forming "clouds", they become invulnerable to grazer control. In the Everglades, new algal growth—before calcification and true mat formation—is usually dominated by green algae and diatoms (Van Meter-Kasanof 1973) and thus may be more susceptible to herbivory than older, more calcified periphyton mats dominated by filamentous cyanobacteria.

Concluding remarks

Our experiments provided evidence for both negative and positive effects of omnivores on Everglades periphyton. These effects could only be revealed by use of an experimental design that allowed at least partial uncoupling of some effects. We believe that our study exposes several general issues for analyses of food-web interactions. First, the impact of omnivores as potential translocators of matter and energy among different compartments of the ecosystem (e.g., nutrient subsidies to primary producers) can be more important than previously thought. Second, edibility of primary producers should be evaluated in studies of consumer-resource interactions because it may be involved in affecting the dynamics of such interactions. Third, herbivory should be analyzed with caution because omnivore-mediated stimulatory effects could compensate for consumption. Studies lacking proper tests for nutrient-mediated effects only document the net effect of con-

sumers, possibly underestimating the total impact of consumers on primary producers. We believe that one implication of overlooking stimulatory effects and documenting only net effects is that disturbances and environmental perturbations that shift the relative abundances of consumers may lead to unanticipated changes in trophic structure by altering unappreciated patterns of nutrient flow to primary producers.

Acknowledgements We thank Ron Jones and the Southeastern Environmental Research Center (SERC) for processing nutrient samples, and Sue Perry for assistance and support. Thanks to the 23 people who helped with fieldwork, making this project possible. We thank J.H. Chick who provided help with several conceptual areas of this project. We also greatly appreciate the comments of C. Osenberg, which improved this manuscript considerably. This work was funded by cooperative agreement number CA5280-8-9002 between Everglades National Park and Florida International University, and a fellowship to P. Geddes from the FIU Tropical Biology Program. This is SERC contribution 199 and 61 of the FIU Tropical Biology Program.

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