Hydrobiologia (2006) 569:375–386

J.C. Trexler, E.E. Gaiser & D.L. Childers (eds), Interaction of Hydrology and Nutrients in Controlling Ecosystem Function in Oligotrophic Coastal Environments of South Florida
DOI 10.1007/s10750-006-0143-y

# Exploring the role of large predators in marsh food webs: evidence for a behaviorally-mediated trophic cascade

Nathan J. Dorn[1,2,*], Joel C. Trexler[1] & Evelyn E. Gaiser[1]
[1]*Department of Biological Sciences, Florida International University, Miami, FL 33199, USA*
[2]*Present address: Department of Biological Sciences, Florida Atlantic University, Davie, FL 33314, USA*
*(*Author for correspondence: E-mail: ndorn1@fau.edu)*

*Key words:* effect size, food web, grass shrimp, macroinvertebrates, predation, trophic cascade, wetland

## Abstract

The influence of large predators on lower trophic levels in oligotrophic, structurally complex, and frequently disturbed aquatic environments is generally thought to be limited. We looked for effects of large predators in two semi-permanent, spikerush-dominated marshes by excluding large fish (>12 mm body depth) and similarly sized herpetofauna from 1 $m^2$ cages (exclosures) for 2 weeks. The exclosures allowed for colonization by intermediate (in size and trophic position) consumers, such as small fish, shrimp, and crayfish. Exclosures were compared to control cages that allowed large fish to move freely in and out. At the end of the experiment, intermediate-consumer densities were higher in exclosures than in controls at both sites. Decapod crustaceans, especially the riverine grass shrimp (*Palaemonetes paludosus*), accounted for the majority of the response. Effects of large fish on shrimp were generally consistent across sites, but per capita effects were sensitive to estimates of predator density. Densities of intermediate consumers in our exclosures were similar to marsh densities, while the open controls had lower densities. This suggests that these animals avoided our experimental controls because they were risky relative to the surrounding environment, while the exclosures were neither avoided nor preferred. Although illuminating about the dynamics of open-cage experiments, this finding does not influence the main results of the study. Small primary consumers (mostly small snails, amphipods, and midges) living on floating periphyton mats and in flocculent detritus (“floc”) were less abundant in the exclosures, indicative of a trophic cascade. Periphyton mat characteristics (i.e., biomass, chlorophyll *a*, TP) were not clearly or consistently affected by the exclosure, but TP in the floc was lower in exclosures. The collective cascading effects of large predators were consistent at both sites despite differences in drought frequency, stem density, and productivity.

## Introduction

Aquatic populations and communities are often assumed to be limited and/or structured by large-bodied fish and other consumers (e.g., Carpenter & Kitchell, 1993; Persson, 1999). The manifestation of top-down effects, however, may be influenced by ecosystem type (Shurin et al., 2002), system productivity (Pace et al., 1999; Benndorf et al., 2002), disturbance frequency (Menge & Olson, 1990; Wellborn et al., 1996), food-web structure (Mittelbach et al., 1995; Vander Zanden et al., 2005), and habitat complexity (Diehl, 1992). Models and empirical studies indicate that top-down influences of large predators should be weakest in oligotrophic, stressful (highly disturbed), and structurally complex environments (Menge & Olson, 1990; Diehl, 1992; Power, 1992; Wellborn et al., 1996).

The oligotrophic freshwater marshes of the Everglades have annual wet and dry seasons and are characterized by dense emergent vegetation.

The trophic structure of the Everglades is unusual in that fish and invertebrate densities are quite low relative to the abundance of periphyton mats (Turner et al., 1999). The effect of large aquatic predators (i.e., large fish and herpetofauna) on Everglades' prey communities is currently unresolved, and has been debated in the literature (Kushlan, 1987; Loftus & Eklund, 1994; Trexler et al., 2005). Hypotheses regarding the weak effects of large fish (>8 cm standard length, SL) on prey assemblages are related to the abundant vegetation (high stem density) that provides cover for prey, as well as the oligotrophic conditions, and repeated droughts that limit densities of both small and large fish (Loftus & Eklund, 1994; Chick et al., 2004; Trexler et al., 2005).

Here we report results from an experimental field study designed to measure the influence of large predators at a 1 $m^2$ scale. Because the Everglades food web is characterized by the presence of many omnivores, we used a size-based manipulation that simplified the food web under the assumption that most similarly-sized large animals function as predators or omnivores that prey upon smaller animals. This assumption is reasonable given the intractable nature of dissecting species-rich food webs via pairwise interactions (Polis & Strong, 1996), and because body-size relationships are generally good predictors of predator-prey relations in aquatic communities (Diehl, 1993; Layman & Winemiller, 2004). For example, fish predators do not discriminate between potential prey based on prey diets (e.g., carnivorous vs. herbivorous invertebrates), but rather on the size of the prey relative to their own gape (Diehl, 1993). Extensive gut content analyses indicate that all large fish in the Everglades include some animal prey in the diets, and most are primarily carnivores (Loftus, 2000).

We investigated the effects of large predators on intermediate consumers and lower trophic levels by excluding all animals larger than 12 mm body depth (i.e., most fish > 8 cm SL) from 1 $m^2$ exclosures for 2 weeks. At the end of the experiment we collected all intermediate consumers (mostly small fish and decapods), and sampled primary consumers (smaller invertebrates), and basal resources (periphyton and flocculent detritus) from exclosures and controls. We report cascading effects in the aggregated food web and then explore the response of the intermediate consumers in greater detail. Differences in intermediate-consumer densities could have been caused by habitat discrimination or survival in the experimental units, and we consider both mechanisms in the discussion.

## Methods

### *Study sites and food web description*

We initiated a food-web experiment in March 2004 in two marshes near SRS 2 and 3 in Shark River Slough (Everglades National Park, Fig. 1). Site 2 is upstream and north of 3, has lower productivity (Williams, 2004) and dries less frequently than Site 3. The sites are characterized by high densities of emergent spikerush (mostly *Eleocharis* spp.), with Site 3 having especially high densities (Table 1). Water depths vary annually between 0 and 80 cm deep. Site 3 dried (depth <5 cm) in 6 of the previous 10 years while Site 2 dried only once (in 2001) during the same period. The fish and invertebrate communities found at each site are similar, however densities tend to be greater at the naturally productive Site 3 (Table 1, Turner et al., 1999). While catch-per-unit-effort (CPUE) of large fish is seasonally and spatially variable (Chick et al., 2004), CPUE was similar at the two sites prior to the experiment (Table 1).

A conceptual (simplified) Everglades size-based food web can be seen in Figure 2. Large fish assemblages consist mainly of several sunfishes (*Lepomis* spp. and *Micropterus salmoides* Lacepede), Florida gar (*Lepisosteus platyrhincus* De Kay), lake chubsucker (*Erimyzon sucetta* Lacepede), pickerel (*Esox* spp.), yellow bullhead (*Ameiurus natalis* Lesueur) and the non-indigenous Mayan cichlid (*Cichlasoma urophthalmus* Gunther) and blue tilapia (*Oreochromis aureus* Steinachner). Large-bodied herpetofauna such as alligators (*Alligator mississippiensis* Daudin), greater siren (*Siren lacertina* Linnaeus), and pig frogs (*Rana grylio* Stejneger) were also excluded from our experimental cages. Although alligators and pig frogs are known to prey on decapod crustaceans (T. Ugarte, personal communication), their importance in the food web is largely unknown. We will hereafter refer to the excluded

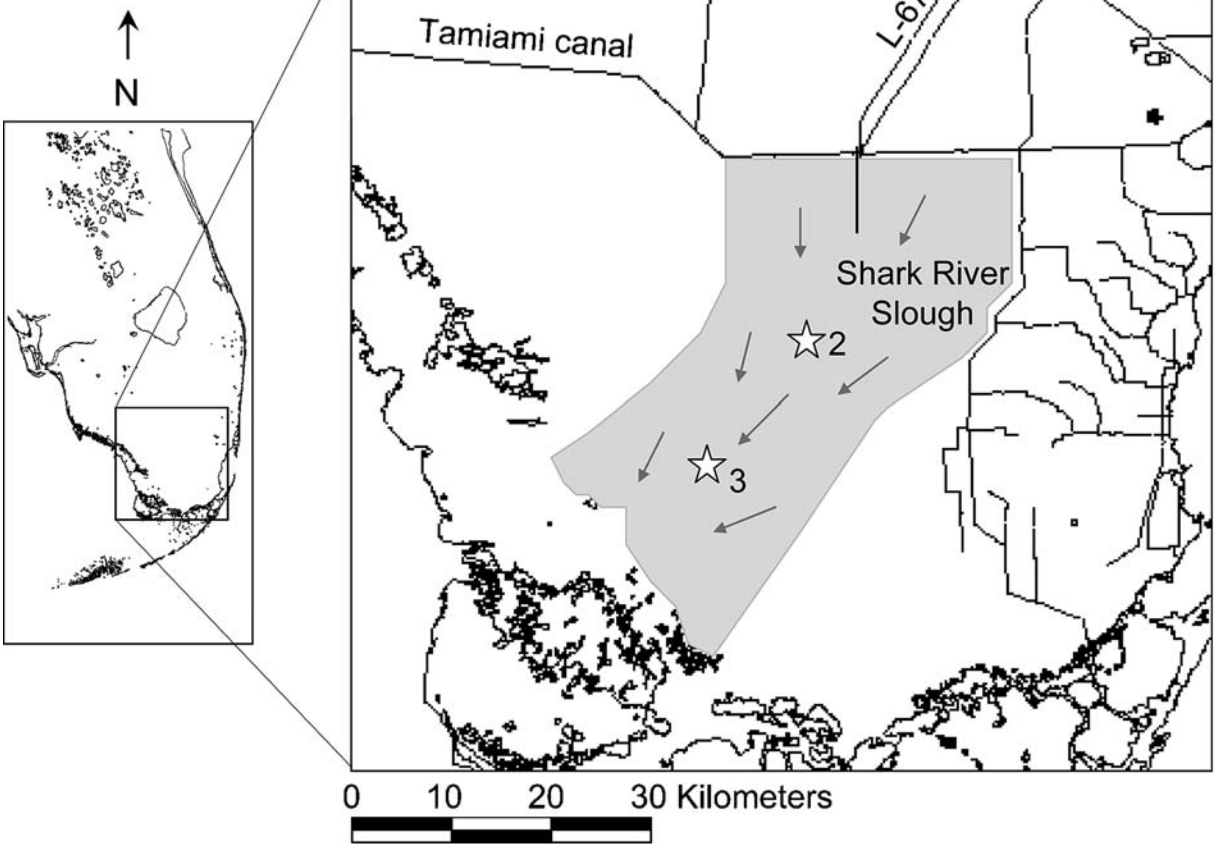

*Figure 1.* Map of experimental sites (LTER sites SRS Site 2 and Site 3) in the Florida Everglades. The highlighted area (shaded) represents the freshwater portion of Shark River Slough in Everglades National Park. Arrows indicate the general flow of water in the slough and dark lines to the east and north are canals. These sampling areas are referred to as Sites 6 and 37 in Trexler et al. (2002).

*Table 1.* Physical and biological parameters (mean + S.E.) at the experimental sites

| Parameter | Site 2 | | Site3 | |
|---|---|---|---|---|
| | February | April | February | April |
| Water depth (cm) | 46.5 (1) | 36.4 (1) | 41.3 (3) | DRY |
| Periphyton biovolume (ml) | 2667 (135) | 2900 (438) | 1133 (446) | 0 |
| Stem density (no./m$^2$) | 138 (5.5) | 158 (11) | 770 (218) | NA |
| Large fish[a] CPUE (no./5 min. bout) | 1 (0.4) | 1.67 (0.9) | 1.44 (0.9) | 0 |
| Small fish[b] density (no./m$^2$) | 11.3 (1.7) | 9.7 (2.1) | 28 (4.5) | 0 |
| Density of large invertebrates (no./m$^2$) | 16.3 (3.6) | 52.9 (7.0) | 89.6 (6.7) | 0 |
| Shrimp density | 13.1 (3.2) | 44.9 (5.8) | 62.6 (6.6) | 0 |
| Crayfish density | 0.6 (0.2) | 1.1 (0.6) | 5 (1.4) | 0 |

[a] Greater than 8 cm standard length.

[b] Less than 8 cm standard length.

animals as “large predators” or “large fish,” and will discuss the impacts of “large fish” in the discussion.

Intermediate consumers in this food web are both intermediate in size and in trophic position. They consist primarily of small fishes, crayfish, and grass shrimp (Fig. 2). A few individuals of other similarly-sized intermediate consumer taxa (e.g., dragonfly naiads) colonized the cages but their numbers were low and we excluded them from the analyses. The assemblage of small fishes (*Gambusia holbrooki* Girard, *Heterandria formosa* Agassiz, *Lucania goodei* Jordan, *Fundulus chrysotus* Günther, juvenile *Erimyzon sucetta* Lacepede, *Noturus gyrinus* Mitchill, *Lepomis marginatus* Holbrook, *Lepomis punctatus* Valenciennes, and *Aphredoderus sayanus* Gilliams) that colonized the enclosures included mostly carnivores and omnivores (Gunderson & Loftus, 1993) while the slough crayfish (*Procambarus fallax* Hagen) and riverine grass shrimp (*Palaemonetes paludosus* Gibbes) are omnivores. While not all large fish feed on this group of intermediate consumers, we make the simplifying assumption that the functionally dominant relationship between these two groups is one of predator–prey relations (i.e., most bigger fish and herpetofauna feed on intermediate consumers) (Fig. 2), and further, that from a food web perspective, this is a dynamically important interaction. If the assumption is false, or if the interaction is otherwise weak, then we expect to see no difference in intermediate consumer densities between the treatments.

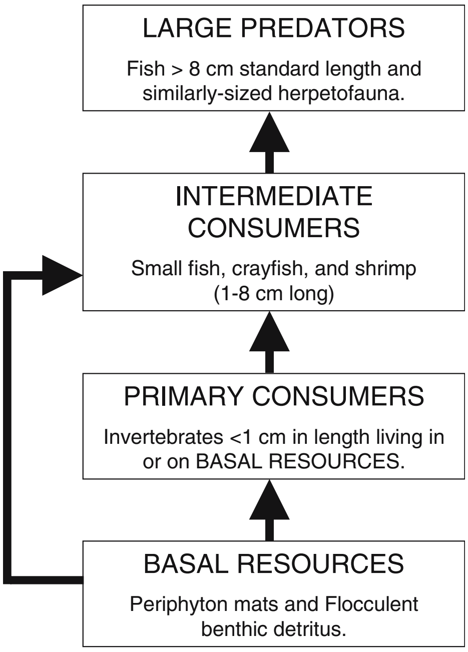

*Figure 2.* Schematic size-based food web for Everglades marshes. Arrows indicate the flow of energy and omnivory between size-based trophic groupings.

This simplified Everglades food web has basal resources of periphyton mats and flocculent detritus (floc) (Fig. 2). The periphyton mats are a complex of live and dead algae, *Utricularia* spp., heterotrophic bacteria, and detritus, which can form large floating mats (Turner et al., 1999). The mats and floc have distinct invertebrate communities (Liston & Trexler, 2005). For the purposes of this paper, we have lumped all of the small invertebrates (mostly small gastropods, amphipods, chironomids, and oligochaetes) residing in or on each of the basal resources into two response variables; primary consumers in periphyton mats and primary consumers in floc. Although there may be some carnivorous members of these groups, we assume that the most are herbivores/detritivores (Fig. 2).

### *Cage experiment*

The experimental cages measured 1 $m^2$ in area, with walls and floors of 2 mm mesh. Each cage contained artificial vegetation (50 black plastic strips, 2.5 cm wide and 50 cm long) to provide cover for the animals. Treatments consisted of two cage types: a cage control (hereafter “control”) with one open side that allowed all consumers, including large predatory fish and herpetofauna, to move in and out, and an exclosure cage (hereafter “exclosure”) with 12 mm mesh on one side that allowed small fishes, shrimp, crayfish and other invertebrates to move freely in and out, while excluding large predators.

The experiments were started on consecutive dates (Site 3 on March 8, and Site 2 on March 9). Water depths were 39 and 37 cm at Sites 2 and 3 respectively, but Site 3 dried completely a month after our experiment ended while Site 2 remained wet throughout the dry season. The cages were arranged perpendicular to the flow of water in 3 blocks (1 replicate per block) at each site ($n$ = 6 across sites). We scored the experiment after 14 days.

*Table 2.* Effects of predator exclosures on intermediate consumers, primary consumers, and basal resources (periphyton and floc) as detected by ANOVA (*F*-statistics and error degrees of freedom shown)

| Source | Intermediate consumers[a] | Periphyton 1° consumers | Floc 1° consumers[b] | Periphyton TP | Periphyton AFDM | Periphyton chl *a* | Floc TP[b] |
|---|---|---|---|---|---|---|---|
| Treatment | 47.2*** | 195.7*** | 68.0* | 4.9‡ | 3.2 | 0.4 | 13.2** |
| Site | 11.9** | 0.8 | 6.6 | 1.0 | 7.8* | 12.1* | 20.8** |
| Site × treatment | 0.5 | 0.3 | 1.0 | 0.0 | 1.5 | 2.3 | 0.7 |
| Block (Site) | – | 64.1*** | 22.7* | 2.9 | 2.1 | 4.7‡ | - |
| Error d.f. | 8 | 4 | 3 | 4 | 4 | 4 | 7 |

Error degrees of freedom differ depending upon whether or not the nested block term was included in the analysis (removed when $p > 0.45$).

‡ $0.05 < p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$.

[a] Fish, shrimp, and crayfish combined.

[b] One or two replicates were lost from the control cages (making $n = 4$ or 5) for these response variables.

We added periphyton mat to each cage at densities similar to densities in the marsh (2 kg wet mass per cage). Large invertebrates and small fish were removed from the periphyton mat prior to addition. To measure the effects of experimental treatments on nutrients and invertebrates in the floc, we added a single tray (170 cm$^2$) with floc (~350 ml) to each cage. Large animals (e.g., shrimp) were removed from the floc prior to placing it in the trays. Trays were open on top so that consumers could forage on the organic material or invertebrates residing therein.

The cages were sealed at the time we scored the experiment, to capture the mobile animals present in the cages. After sealing each cage we used bar seines and aquarium nets to recover the fish, invertebrates, and benthic algae. After 4–8 bar seines per cage, we tipped the cage on a corner to remove the remaining algae and animals by hand and/or aquarium net. We passed our hands through the corners of the cage (through any accumulated sediments) to feel for snails and other remaining animals. Fish, crayfish, shrimp, and other large invertebrates were preserved in 10% formalin (fish were first anesthetized with MS222), and subsequently counted in the lab.

At the termination of the experiment, all algae were removed from the cages, placed in a plastic bag on ice, and transported back to the lab. After draining excess water from the mat samples, we recorded the wet mass of each sample and removed a subsample for further analysis. We first picked out, counted, and identified macroinvertebrates under a dissecting scope. Invertebrates were identified to orders (e.g., Gastropoda) or families (e.g., Chironomidae), but all animals (<1 cm length) were grouped together and analyzed as density of primary consumers per unit dry mass (g) of periphyton mat. The remaining sample of algae and detritus was homogenized in a blender and subsamples were taken for total phosphorous (TP, 120 ml), chlorophyll *a* (1 ml), and measurements of dry/ash weights (40 ml). For chlorophyll *a* analysis, we filtered 1 ml samples onto 25 mm glass fiber filters, placed them in microvials, and extracted chlorophyll *a* with 1.5 ml of 90% acetone in a dark freezer for 20 h. After centrifuging the samples, we used narrow-band fluorometry (Welschmeyer, 1994) to quantify chlorophyll *a* concentration.

We also removed the trays of floc at the end of the experiment. From each tray, we removed one aliquot (~1.5 g after drying) for TP analysis and a second aliquot for invertebrate processing (all animals < 1 cm length). Invertebrate communities were primarily composed of midges (families Chironomidae and Tanypodinae), oligochaetes, and ostracods. Invertebrate densities were expressed as density per unit ash-free dry mass of floc.

### *Statistics*

Response variables for the two sites were analyzed together including "site" and "block nested within site" as fixed effects in linear models. Sites were

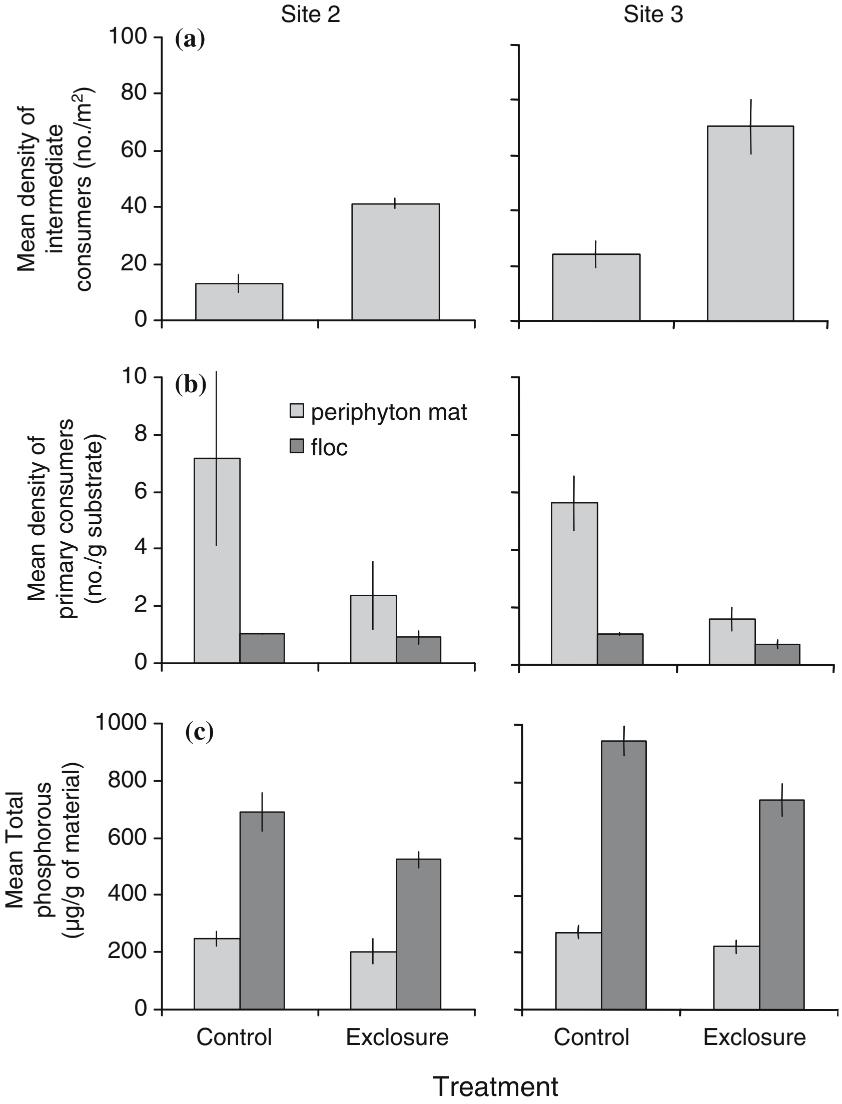

*Figure 3*. Responses of three trophic levels to manipulation of large predators in Everglades marshes. (a) Densities of total intermediate-sized consumers (fish, shrimp, and crayfish). (b) Densities of primary consumers (amphipods, midges, and snails) living in floc and periphyton mats. (c) Phosphorous content of floc and periphyton mats. Error bars represent 1 S.E. See Table 2 for statistics.

treated as fixed effects because they were specifically chosen to represent areas of naturally high and low productivity (Littell et al., 2002, p. 425). Where block(site) was non-significant ($p > 0.45$), it was dropped from the final analysis. Total intermediate-consumer densities were analyzed with ANOVA (density of decapods and fish together).

Analyses of primary consumers found in floc and periphyton mats were performed with individual ANOVAs, and responses of the two basal resources were analyzed separately with 2 tests: MANOVA was used for the 3 periphyton response variables and floc TP was analyzed with ANOVA. Response variables were $\log_{10}$ or square-root transformed when necessary to normalize residuals.

We looked for treatment effects and site × treatment interactions on the three intermediate-consumer taxa (fish, shrimp, and crayfish)

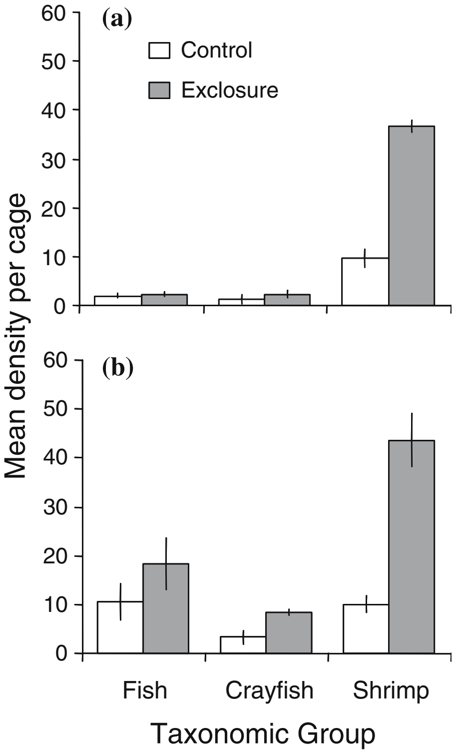

*Figure 4.* Mean number of the 3 most common intermediate-sized consumer groups recovered from cage controls and exclosure cages at Site 2 (a) and Site 3 (b) in Everglades National Park. Error bars represent 1 S.E.

separately with multivariate ANOVA (MANOVA). We also calculated effect sizes of large predators on grass shrimp (the most abundant intermediate consumer) for each block at each site, to test for inter-site variation in predator effects. We used 2 indices reviewed by Berlow et al. (1999), the dynamic index [DI = $\ln(N_c/N_e)$, see also Osenberg et al., 1997] and the raw difference (RD = $N_c - N_e$; where $N_c$ = density in control and $N_e$ = density in exclosure), and compared collective effects and per-capita effects (dividing each effect by large fish abundance at each site). Large-fish abundance can be estimated different ways, and the calculation of per capita effects is sensitive to the quality of the estimates (Berlow et al., 1999). We estimated large-fish abundance with the raw CPUE (Table 1) and by estimation of density (#/0.1 ha) (extricated from the CPUE vs. density relationship in Chick et al., 1999; 8/ha at Site 2 vs. 18/ha at Site 3). Because the relationship between CPUE and density is not proportional (density increases proportionally faster than CPUE), differences in predator abundance between the sites were greater when converted to density. Effect sizes measured with DI are probably the most appropriate measure for such a short-term colonization experiment, with populations starting far from equilibrium (zero at beginning of this study) (Berlow et al., 1999). For each index we used univariate tests to examine site variation.

We also compared the total intermediate consumer densities in our cages to natural densities in the marsh (samples taken before and after the experiment; see methods in Trexler et al., 2002), to examine the general assumption that exclosures act as refuges in the natural environment. We assumed a linear relationship would best describe the dynamics of total intermediate-consumer densities at Site 2, and estimated a 95% confidence window for total animal density from February through April. Because Site 3 was dry in April, we could only compare cage densities to marsh densities from February.

## Results

We captured two large (>10 cm SL) carnivorous fish (pike killifish, *Belonesox belizanus*, and Mayan cichlid, *Cichlasoma urophthalmus*) in two of the three control cages at Site 3. At Site 2, one of the floc trays placed in a control cage was removed and deposited more than 20 m away, presumably by an alligator (as evidenced by tooth marks). These observations (and similar ones from other studies) indicated that large predators in the marsh used our control cages as foraging areas or as cover, and that exclosures provided a different environment with lower predation risk.

*Table 3.* Effects of large predator exclosures on densities of three intermediate consumer taxa as revealed by ANOVA (*F*-statistics shown)

| Source | d.f. | Fish | Shrimp | Crayfish |
|---|---|---|---|---|
| Treatment | 1 | 1.5 | 115.7*** | 7.1* |
| Site | 1 | 20.6** | 1.0 | 12.3** |
| Site × treatment | 1 | 1.0 | 0.7 | 1.9 |
| Error | 8 | | | |

‡$0.05 < p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.005$.

*Table 4.* Mean (S.E) collective and per-capita effect sizes of large fish on shrimp

| Measure | 2 | 3 | $F_{1,4}$ | $p$ |
|---|---|---|---|---|
| DI | −1.36 (0.2) | −1.47 (0.3) | 0.1 | 0.73 |
| DI/cpue | −1.36 (0.2) | −1.03 (0.2) | 1.6 | 0.28 |
| DI/density | −0.18 (0.02) | −0.08 (0.02) | 10.6 | 0.03 |
| RD | −27.0 (2.1) | −33.7 (6.9) | 0.9 | 0.41 |
| RD/cpue | −27.0 (2.1) | −23.4 (4.8) | 0.5 | 0.53 |
| RD/density | −3.4 (0.3) | −1.9 (0.4) | 10.6 | 0.03 |

DI = $\ln(N_c/N_e)$ and RD = $(N_c - N_e)$. Statistical results from ANOVA.

Exclosures contained a greater total density of intermediate consumers than controls at both sites, and intermediate-consumer densities were higher overall at Site 3 (Table 2, Fig. 3a). Exclosures had lower densities of small primary consumers inhabiting the periphyton mat and floc (Table 2, Fig. 3b). Despite the lower density of primary consumers, the treatment had an inconsistent and/or weak influence on periphyton (MANOVA on three response variables: $F_{3,2}$ = 17.75, $p$ = 0.054) (univariate statistics in Table 2, Fig. 3c). Total phosphorous content of the periphyton mat was reduced 19% in exclosures (Fig. 3c, $p$ = 0.092), but biomass and chlorophyll *a* did not differ (Table 2). Total phosphorus content (both sites) of the benthic floc was reduced by 21% in exclosures (treatment effect: $p$ = 0.008, Table 2, Fig. 3c).

The three taxa of intermediate consumers responded to the exclosures (MANOVA $F_{3,2}$ = 32.77, $p$ = 0.03), by increasing overall densities, but univariate tests indicated that only grass shrimp and crayfish showed a statistically significant response (Fig. 4, Table 3). Fish and crayfish were both more abundant at Site 3 than at Site 2 (Fig. 4, Table 3), and there were no significant interactions between site and treatment (Table 3).

Analyses of most effect sizes were consistent with tests of raw densities (Table 4); the collective effects and per-capita effects calculated using CPUE did not differ between sites. The per-capita effect sizes were smaller at Site 3 (both DI and RD) when we used the estimates of large-fish density (Table 4).

Densities of intermediate consumers in the exclosures at Site 2 were near the estimated (interpolated) mean density of intermediate consumers in the marsh, while density in the controls were 65–70% less than densities in the marsh. Densities in exclosure cages at Site 3 (Fig. 5b) were closest to the densities in the natural marsh in

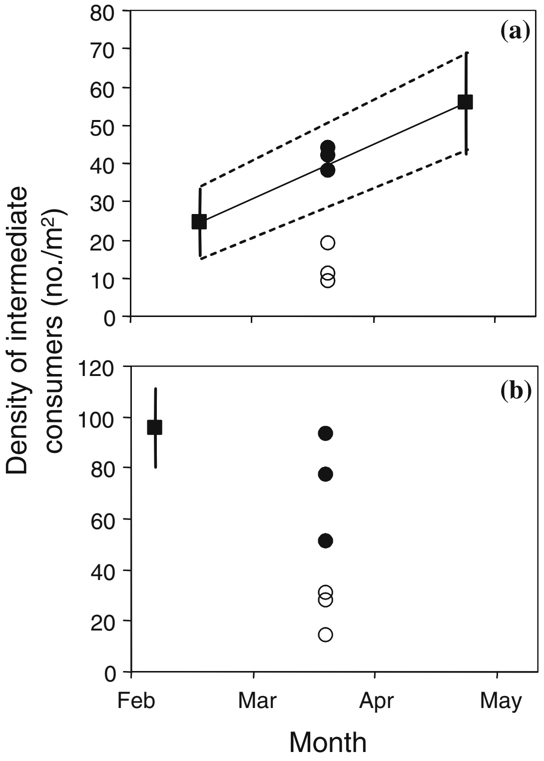

*Figure 5.* Densities of intermediate consumers (all fish, crayfish, and shrimp combined) in the marsh (filled squares) and exclosures (filled circles) and control cages (open circles) at (a) Site 2 and (b) Site 3. Marsh densities are averages and error bars represent 95% confidence intervals ($n$ = 7 estimates). Independent measurements of density were not available for Site 3 in April because the marsh was dry. Trend lines were added to panel (a) to indicate probable changes in animal density over the time period.

February, while densities in the controls were below the densities in the marsh.

## Discussion

Densities of intermediate consumers (i.e., decapods) were higher in exclosure cages than in open control cages, while primary-consumer densities were higher in control cages, consistent with a trophic cascade. Primary producers did not show a clear response to the treatments. In the following paragraphs we consider each trophic link and the mechanisms responsible for the observations.

Differences in decapod densities between exclosure and control cages could have been caused by attraction to the excluder devices as habitat, direct consumption by predators in the control cages, or anti-predator behavior (habitat discrimination). Before we consider each of the potential mechanisms we will address the relationship between the intermediate-consumer densities in the cages and background habitat. The observation that densities in control cages were lower than densities in the marsh, while exclosure densities were similar to marsh densities (Fig. 5), undermines a general expectation about this type of experimental design. Predator exclosures are often assumed to be, or observed to be, ‘‘absolute’’ refuges in predator-exclosure field experiments, while open controls (predators present) are expected to be similar to the un-manipulated background habitat (Englund et al., 2001; Layman & Winemiller, 2004). In our study, the control cages appear to have been riskier or otherwise less attractive than the background habitat, while the exclosures did not appear to act as refuges. These observations suggest that the background habitat and the exclosures were both areas of relatively low predation rates and therefore low risk, while controls attracted predators and were relatively dangerous. Although illuminating about the nature of the experiment, and worthy of additional consideration, these findings do not indicate which mechanism was responsible for the observed differences in decapod densities.

At the beginning of the experiment, both cage types started empty and were colonized as the experiment progressed, so treatment differences were either caused by animal movement (migration) or consumption (mortality in the cage). One alternative to the predation-driven mechanisms is that decapods were attracted to the wire excluder devices as unique or novel habitats. Although we cannot rule this out, if it were an important mechanism, we might have expected decapods to be clinging to the wire mesh when we approached the cages to seal them. We have never observed shrimp or crayfish in such a position. If density differences were driven entirely by consumption in the control cages, we must assume that decapods moved in and out of both cage types without discrimination (no anti-predator behavior) and that fish predators ate them in the control cages, effectively lowering their densities. Although we find the assumption of indiscriminant movement unlikely, we cannot rule it out with the available data. The behavioral ecology of decapods and theoretical considerations about the scale of this experiment suggest that the differences were at least partially caused by behavioral avoidance of the control cages. Several studies indicate that both shrimp and crayfish actively seek shelter from large fish predators (Ruiz et al., 1993; Garvey et al., 1994; Jordan et al., 1996; and others). Crayfish, in particular, have acute chemosensory facilities that help them assess predation risk (Bouwma & Hazlett, 2001), and exhibit habitat associations that lower the risk of fish predation in lakes (Lodge & Hill, 1994). Taken together, these observations lead us to believe that an assumption of indiscriminant habitat use/movement by decapods is incorrect for this study.

The spatial scale of the experiment also affects the consideration of behavior- vs. consumption-driven mechanisms. When predator exclosures are small relative to the daily movement rates of the prey, theoretical work predicts cage dynamics dominated by prey movement (i.e., behavior) (Englund, 1997; Englund et al., 2001). We believe the conditions laid out by Englund (1997), for movement-dominated dynamics, were satisfied in our study; the shrimp and crayfish in this study (body lengths 1–5 cm) probably move more than one length of the cage (1 m) per day. Thus, we believe the behavior-driven mechanism more plausible than the consumption mechanism. Though it is likely that both contributed to patterns we observed, further studies would be necessary to tease apart their relative importance.

Although our exclosures failed to act as absolute refuges, our observation of the trophic cascades at both study sites remain informative and realistic, especially because the indirect effect of large predators on primary consumers were not mediated by exorbitant (unnaturally high) shrimp densities in the exclosure cages. Instead, mat-dwelling primary consumers were maintained at higher densities in the control cages as a result of lower shrimp densities. These data suggest that periphyton mat-dwelling invertebrates are released from predation in areas with fewer shrimp (see also Liston, 2006). We expect that densities of primary consumers in the mats of the undisturbed marsh would have been similar to densities in the exclosures. Unfortunately, we did not collect invertebrates from undisturbed mats during the study and could not check this hypothesis further.

Earlier work by Geddes & Trexler (2003) found a positive relationship between intermediate consumer (shrimp and fish) density and periphyton mat growth (TP, AFDM, etc.). This contrasts with the lack of responses in our study. However, Geddes & Trexler (2003) reported three separate experiments and in the experiment most similar to our study (late dry season in Shark River Slough), they found no net positive effects of intermediate consumers on the periphyton mat. It is also likely that there is significant spatial and seasonal variation (e.g., the dry season is dominated by algal senescence) in consumer effects on the algal mat, underscoring the importance of replicating experiments in space and time.

In general, predator effects attenuate as they move through the food web (Shurin et al., 2002) and this could explain weak/inconsistent responses by the algal mat in this study. The intermediate consumers in this study, which are omnivores, complicate predictions of trophic cascades by feeding on both primary consumers and the periphyton mat (Polis & Strong, 1996; Geddes & Trexler, 2003; Dorn & Wojdak, 2004). The direction of the floc TP response indicates that the decapods were milling through the benthic sediments and selectively ingesting high-quality (P rich) food. This explanation is consistent with several other studies that indicate decapods play a significant role in organic matter processing (Crowl et al., 2001; Usio & Townsend, 2002).

### *Effects of large predators in Everglades marshes*

Food-web theory suggests that oligotrophic and frequently disturbed environments should have fewer top predators, and weaker top-down effects, than more permanent environments (Menge & Olson, 1990). While the Everglades marshes are naturally oligotrophic and have annual drying cycles, we do not currently know where these Everglades freshwater marshes fall along this continuum. Kushlan (1987) argued that the current altered ecosystem has more large fish predators (and a larger effect of piscivores) than the historic system, but Loftus & Eklund (1994) refuted the earlier work and argued that both small and large fish are limited by drought. Trexler et al. (2005) re-analyzed the historic data and developed a conceptual model suggesting that predator effects will begin to outweigh effects of disturbance on small fish density after 5–8 years of constant inundation. Based on that model, fish communities at most sites in the Everglades marshes should be in recovery (population growth) phases most of the time. The sites where we performed this experiment dried 2–3 years prior to the study, suggesting that the lack of response by fish in these experiments could have been caused by a paucity of large fish. The responses by shrimp and crayfish suggest that decapods may be more sensitive to large fish than the contemporaneous fish assemblage.

Collective predator effects indicated by comparisons of actual densities or effect sizes (DI or RD) were consistent between sites, despite differences in hydrology, vegetation, and productivity. However, when we computed per-capita effects, a different result emerged. The effects of large predators on shrimp, on a per predator basis were less at Site 3 than at Site 2 when we used large fish density estimates, but not when we used CPUE. Given the high variation in density estimates possible for these CPUE values (Chick et al., 1999), we hesitate to discuss the difference between the sites. Nevertheless, the contradictory results highlight the importance of obtaining robust density estimates in order to make meaningful conclusions about per-capita effect sizes.

## Conclusion

In spite of the oligotrophic conditions, high stem densities, and annual drying cycles, we found evidence that large fish can have important effects on decapod densities at the 1-m$^2$ scale in Everglades marshes. This effect indirectly reduced small primary consumers dwelling in the periphyton mats (presumably a linear cascade) and lowered TP in the flocculent sediments. How these trophic interactions scale up to affect population regulation or community structure is unknown, but this represents one of the first Everglades field studies indicating an important effect of large aquatic predators. The influences of large predators and intermediate consumers in freshwater Everglades marshes are not fully resolved, and will require greater attention to predict effects of hydro-management and restoration scenarios.

## Acknowledgements

Thanks to P. Geddes, B. Loftus, and other reviewers who made helpful critical suggestions on a penultimate draft of this paper. This work was funded through a cooperative agreement between Everglades National Park and Florida International University (H5284030034) and the Florida Coastal Everglades LTER project (NSF 99-10514). This is contribution #306 of the Southeast Environmental Research Center at Florida International University.

## References

Benndorf, J., W. Böing, J. Koop & I. Neubauer, 2002. Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. Freshwater Biology 47: 2282–2295.

Berlow, E. L., S. A. Navarrete, C. J. Briggs, M. E. Powers B. A. Menge, 1999. Quantifying variation in the strengths of species interactions. Ecology 80: 2206–2224.

Bouwma, P. & B. A. Hazlett, 2001. Integration of multiple predator cues by the crayfish *Orconectes propinquus*. Animal Behavior 61: 771–776.

Carpenter, S. R. & J. F. Kitchell, 1993. The Trophic Cascade in Lakes. Cambridge University press, Cambridge, MA, USA.

Chick, J. H., S. Coyne & J. C. Trexler, 1999. Effectiveness of airboat electrofishing for sampling fishes in shallow, vegetated habitats. North American Journal of Fisheries Management 19: 957–967.

Chick, J. H., C. R. Ruetz & J. C. Trexler, 2004. Spatial scale and abundance patterns of large fish communities in freshwater marshes of the Florida Everglades. Wetlands 24: 652–664.

Crowl, T. A., W. H. McDowell, A. P. Covich & S. L. Johnson, 2001. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. Ecology 82: 775–783.

Diehl, S., 1992. Fish predation and benthic community structure – the role of omnivory and habitat complexity. Ecology 73: 1646–1661.

Diehl, S., 1993. Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. Oikos 68: 151–167.

Dorn, N. J. & J. M. Wojdak, 2004. The role of omnivorous crayfish in littoral communities. Oecologia 140: 150–159.

Englund, G., 1997. Importance of spatial scale and prey movements in predator caging experiments. Ecology 78: 2316–2325.

Englund, G., S. D. Cooper & O. Sarnelle, 2001. Application of a model of scale dependence to quantify scale domains in open predation experiments. Oikos 92: 501–514.

Garvey, J. E., R. A. Stein & H. M. Thomas, 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. Ecology 75: 532–547.

Geddes, P. & J. C. Trexler, 2003. Uncoupling of omnivore-mediated positive and negative effects on periphyton mats. Oecologia 136: 585–595.

Gunderson, L. H. & W. F. Loftus, 1993. The Everglades. In Martin, W. H., S. G. Boyce & A. C. Echternact (eds), Biodiversity of the Southeastern United States: Lowland. John Wiley & Sons, New York, 199–255.

Jordan, F., C. J. DeLeon & A. C. McCreary, 1996. Predation, habitat complexity, and distribution of the crayfish *Procambarus alleni* within a wetland habitat mosaic. Wetlands 16: 452–457.

Kushlan, J. A., 1987. External threats and internal management: the hydrologic regulation of the Everglades, Florida, U.S.A. Environmental Management 1: 109–119.

Layman, C. A. & K. O. Winemiller, 2004. Size-based responses of prey to piscivore exclusion in a species-rich neotropical stream. Ecology 85: 1311–1320.

Liston, S. E., 2006. Interactions between nutrient availability and hydroperiod shape macroinvertebrate communities in Florida Everglades marshes. Hydrobiologia 569: 343–357.

Liston, S. E. & J. C. Trexler, 2005. Spatio-temporal patterns in community structure of macroinvertebrates inhabiting calcareous periphyton mats. Journal of the North American Benthological Society 24: 832–844.

Littell, R. C., W. W. Stroup & R. J. Freund, 2002. SAS for Linear Models. SAS Publishing, Cary, NC, USA.

Lodge, D. M. & A. M. Hill, 1994. Factors governing species composition, population size, and productivity of cool-water crayfishes. Nordic Journal of Freshwater Research 69: 111–136.

Loftus, W. F., 2000. Accumulation and fate of mercury in an Everglades aquatic food web. Ph.D. Dissertation, Florida International University, 295 pp.

Loftus, W. F. & A. M. Eklund, 1994. Long-term dynamics of an Everglades small-fish assemblage. In Davis, S. M. & J. H. Ogden (eds), Everglades: the Ecosystem and its Restoration. St. Lucie Press, Delray Beach, FL, 461–483.

Menge, B. A. & A. M. Olson, 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution 5: 52–57.

Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig & C. W. Osenberg, 1995. Perturbation and resilience: a long-term whole-lake study of predator extinction and reintroduction. Ecology 76: 2347–2360.

Osenberg, C. W., O. Sarnelle & S. D. Cooper, 1997. Effect size in ecological experiments: the application of biological models in meta-analysis. The American Naturalist 150: 798–812.

Pace, M. L., J. J. Cole, S. R. Carpenter & J. F. Kitchell, 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14: 483–488.

Persson, L., 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. Oikos 85: 385–397.

Polis, G. A. & D. R. Strong, 1996. Food web complexity and community dynamics. American Naturalist 147: 813–816.

Power, M. E., 1992. Habitat heterogeneity and the functional significance of fish in river food webs. Ecology 73: 1675–1688.

Ruiz, G. M., A. H. Hines & M. H. Posey, 1993. Shallow-water as a refuge habitat for fish and crustaceans in nonvegetated estuaries – an example from Chesapeake bay. Marine Ecology Progress Series 99: 1–16.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper & B. S. Halpern, 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5: 785–791.

Trexler, J. C., W. F. Loftus, F. Jordan, J. H. Chick, K. L. Kandl, T. C. McElroy & O. L. Bass Jr., 2002. Ecological scale and its implications for freshwater fishes in the Florida Everglades. In Porter, J. W. & K. G. Porter (eds), The Florida Everglades, Florida Bay, and Coral Reefs of the Florida Keys: an Ecosystem Sourcebook. CRC Press, New York, 153–181.

Trexler, J. C., W. F. Loftus & S. Perry, 2005. Disturbance frequency and community structure in a twenty-five year intervention study. Oecologia 145: 140–152.

Turner, A. M., J. C. Trexler, C. F. Jordan, S. J. Slack, P. Geddes, J. H. Chick & W. F. Loftus, 1999. Targeting ecosystem features for conservation: standing crops in the Florida Everglades. Conservation Biology 13: 898–911.

Usio, N. & C. R. Townsend, 2002. Functional significance of crayfish in stream food webs: roles of omnivory, substrate heterogeneity, and sex. Oikos 98: 512–522.

Vander Zanden, M. J., T. E. Essington & Y. Vadeboncoeur, 2005. Is pelagic top-down control in lakes augmented by benthic energy pathways? Canadian Journal of Fisheries and Aquatic Sciences 62: 1422–1431.

Welschmeyer, N. A., 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. Limnology and Oceanography 39: 1985–1992.

Wellborn, G. A., D. K. Skelly & E. E. Werner, 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27: 337–363.

Williams, A. J., 2004. Effect of productivity and hydroperiod on food-chain length in the Everglades, Thesis, Florida International University, Miami, Florida, USA.