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Do small-scale exclosure/enclosure experiments predict the effects of large-scale extirpation of freshwater migratory fauna?

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Abstract A variety of theoretical and empirical studies indicate that the abilities of small-scale experiments to predict responses to large-scale perturbations vary. Small-scale experiments often do not predict the directions of large-scale responses, and relatively few empirical studies have examined whether small-scale experiments predict the magnitudes of large-scale responses. Here we present an empirical example of small-scale manipulations predicting not only the directions but also the magnitudes of the effects of whole-catchment, decades-long decimation of migratory freshwater shrimp populations. In streams of Puerto Rico (USA), we used arena sizes of < 2 m^2 in 1- to 4-week exclosure/enclosure experiments. Effects of small-scale experiments largely matched those of large-scale shrimp loss above dams for a variety of response variables (abiotic and biotic factors including epilithic fine sediments, algae and organic matter, and invertebrate grazers, detritivores, and predators). The results of our extrapolation contrast with studies of small- versus large-scale perturbations in the temperate zone. Our findings are likely explained by: a set of response variables that are more dominated by within-patch processes than exchange processes, an experimental manipulation that encompassed the characteristic scales of response variables, our use of open arenas lacking cage artifacts, and/or our combination of two distinct experimental approaches (exclosures and enclosures). Based on our study design, we suggest that extrapolation across experimental scales can be greatly enhanced by embedding open arenas within large-scale conditions that represent all treatment levels.

Keywords Freshwater shrimps · Puerto Rico · Spatial scales · Temporal scales · Tropical stream

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Introduction

The duration and size of most ecological experiments are short and small in comparison to the spatial and temporal scales of impacts that they are designed to mimic (Petersen et al. 2003; Tilman 1989). A key question in both basic and applied ecology is: can we extrapolate results from these logistically feasible and easily replicated manipulations to larger scales? Relatively few studies have examined the ability of small-scale experiments to predict magnitudes of effects in large-scale perturbations (Kohler and Wiley 1997; Englund and Cooper 2003). Most multiscale research has examined whether small-scale experiments predict

the directions of large-scale effects, and results have been mixed (e.g., Brown and Munger 1985; Carpenter 1996; Peckarsky et al. 1997; Gardner et al. 2001; Slavik et al. 2004). Small-scale experiments also offer insight into mechanisms and process rates (e.g., feeding, excretion) used to determine the influence of small-scale phenomena on large-scale patterns (Huston 1999). When small-scale experiments fail to predict the directions of large-scale effects, they can lead researchers to inaccurate conclusions and hypotheses about large-scale perturbations. They can also distract policy-makers into making decisions based on false premises, particularly because management issues generally operate on scales much larger than those of typical experiments (Schindler 1998; Schmitz 2005).

Although small-scale exclosures/enclosures are powerful tools in studies of consumer effects in aquatic food webs (e.g., Flecker 1996), they can fail to predict effects of large-scale consumer perturbations, for a variety of reasons. For example, discrepancies between small- and large-scale manipulations in lakes can be explained by reduced heterogeneity in mesocosms and the long response time of indirect effects (Sarnelle 1997). Different effects of small- and large-scale stream perturbations may result from (1) exchange between treatment areas and large unmanipulated areas surrounding arenas (causing different responses compared with when an entire stream receives the treatment; (2) the impossibility of large-scale processes (e.g., seston export) operating in small patches over short time scales (Cooper et al. 1998; Englund 1997). Scale effects can also be caused by a combination of nonlinearity and scale-dependent heterogeneity (e.g., Bergstrom and Englund 2004; Melbourne and Chesson 2005; Rastetter et al. 1992). Similar mechanisms of scale dependence operate in marine/estuarine experiments (Gardner et al. 2001).

Here we document the capability of small ($< 2 \text{ m}^2$), short-term (1–4 weeks) exclosure and enclosure experiments to predict not only the directions but also the magnitudes of the effects of whole-catchment, decades-long faunal loss above dams in neotropical streams of Puerto Rico. Small-scale experiments have repeatedly shown that freshwater shrimps decrease epilithic algae, organic matter, and sediments, increase leaf decay, and affect chironomid and mayfly biomass (e.g., March et al. 2002; Pringle et al. 1999; and references therein). However, the extent to which these effects extrapolate to larger scales of shrimp loss are poorly known. Limited surveys of stream reaches varying in shrimp abundances naturally (Pringle et al. 1999) and due to harvest

(E. Greathouse, C. Pringle, N. Hemphill, E. García, W. McDowell, J. March, and A. Ramírez, unpublished manuscript) have provided evidence that small-scale exclusions accurately predict the directions of impacts on benthic resources at large scales of shrimp removal, but they examined neither nondecapod invertebrates nor magnitudes of effects. We hypothesized that small-scale experiments would predict directions of effects, but underestimate magnitudes of effects in the large-scale perturbation due to dams, particularly for nondecapod invertebrates.

Materials and methods

Background and rationale

We worked in pools of high-elevation mountain streams (see Appendix 1 in Electronic Supplementary Material). Freshwater shrimps (*Atya*, *Xiphocaris*, *Macrobrachium*) dominate these habitats in terms of biomass and ecological interactions (Covich and McDowell 1996). Typical densities are high (~20–25 shrimp m^{-2}, E. Greathouse, unpublished data). A single native fish species, an algivorous goby (*Sicydium plumieri*), also occurs in these habitats, but at fewer sites and at much lower densities (0–3 *Sicydium* m^{-2}, Greathouse and Pringle 2006). Effects of *Sicydium* are thought to be qualitatively similar to those of shrimps because of their similar feeding behavior (scraping epilithon), yet quantitatively much lower due to their low densities. The ecological effects of *Sicydium* have not been fully elucidated because experiments (including those in this paper) have either manipulated shrimps only or the presence/absence of the entire macroconsumer assemblage.

Freshwater shrimps (and *Sicydium*) in Puerto Rico are diadromous (i.e., migratory, between fresh and salt water). Because large dams (height > 15 m) block diadromous migrations, shrimp and *Sicydium* populations in free-flowing streams upstream from large reservoirs are decimated (Holmquist et al. 1998). This alteration of shrimp populations in turn has strong effects in pools that match the overall qualitative predictions of previous small-scale experiments (Greathouse et al. 2006). Greathouse et al. (2006) found that pools above large dams had high levels of epilithic algae, sediments, organic matter, and nondecapod invertebrates, but in sites without large dams (matched with dammed sites for physical habitat and water chemistry), pool rocks were grazed clean. To quantitatively compare the effects of large-scale shrimp loss with the effects of small-scale manipulations, we conducted experiments

in pools of a subset (two dammed, two undammed) of the 17 high-gradient sites surveyed by Greathouse et al. (2006).

Study sites, experimental treatments, and scale comparisons

The experimental sites are representative of the 17 survey sites in terms of physical habitat and water chemistry (Greathouse 2005). Steep boulder/bedrock cascades alternate with still-water plunge pools, also containing substantial amounts of boulder and bedrock. Stream temperatures and flows show only slight seasonal variation; flash floods with discharge increases up to 10-fold in less than an hour occur throughout the year (Covich and McDowell 1996). Dams from the survey are located ~2–20 km downstream from headwaters and were built ~30–90 years prior to 2003.

At the two undammed sites, we used electricity to exclude macroconsumers from boulders/bedrock in pools. Excluded macroconsumers were primarily high densities of shrimps, but also included low densities of *Sicydium* and nonmigratory fauna (crabs and tadpoles > 1.5 cm in length). Tadpoles < 1.5 cm in length and nondecapod invertebrates were not excluded. At the two dammed sites, we conducted enclosure experiments in pools, adding shrimps to boulder/bedrock areas (~1.5 m^2) enclosed by block nets. Effectiveness of exclosure and enclosure treatments was ensured by conducting observations. Response variables measured were epilithic standing stocks of: chlorophyll *a*; fine benthic inorganic matter (FBIM; < 1 mm); fine benthic organic matter (FBOM); total carbon (C), nitrogen (N), and C:N ratio of FBOM; coarse benthic organic matter (CBOM; > 1 mm); and nondecapod invertebrate biomass.

Electric exclusion experiments

Macroconsumers (shrimps, fishes, tadpoles, crabs) were excluded from individual boulders and from small areas of bedrock in still-water pools (Greathouse 2005 site codes: U4 [nine pools]; U5 [seven pools]). For electric exclusion methods and apparatus, we used the technique of Pringle and Blake (1994) and Pringle et al. (1999). In each site, 16 wooden hoops served as templates for 12-gauge stranded copper wire and were attached to boulders or bedrock. Eight hoops were randomly chosen to be electric exclusion treatments in which wires were connected to electric fence chargers (Parker-McCrory 12-V, Kansas City, MO, USA) on the bank. The other eight hoops were unelectrified controls allowing macroconsumer access; control hoop wires were tied to riparian trees. Within sites, electric treatments and unelectrified controls did not differ in terms of water depth (*P* values > 0.6), water velocity (*P* values > 0.3) or canopy cover (*P* values > 0.5; one-way ANOVAs).

We turned on electricity at site U4 on 2nd June 2002 and site U5 on 31st March 2003. All "day 0" sampling occurred prior to turning on fence chargers. In a large flood, which occurred 2 days after applying electricity at site U4, hoops were crushed or washed downstream. We reattached and replaced washed-out hoops and applied electricity on 10, 19, and 21 June 2002. For these hoops, we used these dates as day 0 to determine all sampling days except for day 0 (e.g., for the hoops with electricity applied on 10 June, day 10 sampling was on 20 June, but "day 0" data was still from 2 June). We sampled epilithic chlorophyll *a*, FBIM, and FBOM using a suction device modified from Loeb (1981). Sampling methods and apparatus for CBOM (quantitative) and nondecapod invertebrates (semi-quantitative, i.e., biomass per unit effort) are described by Greathouse and Pringle (2005). We Loeb sampled on days 0, 10, 15, 20, and 25 (at site U4) or 27 (at site U5) and sampled nondecapod invertebrates and CBOM on days 15 and 25 (site U4) or 27 (site U5). We randomly chose half of the replicates to run shorter than the other half, as a trade-off between longer running treatments and the risk of floods washing out hoops. Thus, replicates destructively sampled on day 15 for nondecapod invertebrates and CBOM were not sampled again. For each replicate, C and N were only analyzed on one day, generally the last sampling day. Laboratory processing of all samples followed methods described by Greathouse et al. (2006). For statistical analyses, when response variables were measured over time within a single hoop, we reduced these repeated measures to the experimental unit by averaging to obtain a single value (Gotelli and Ellison 2004). These averages did not include day 0 data, which showed no differences between electric treatments and unelectrified controls within sites (*P* values > 0.24, one-way ANOVAs).

Effectiveness of exclusions was ensured by conducting timed observations. Daytime observations consisted of counting all macroconsumers entering a hoop during each 30-s interval of a 10-min period. Night time observations using red-filtered flashlights followed the same protocol for a 5-min period. At site U4, we only conducted observations on control hoops because the U4 macroconsumer community is characteristic of other streams in Puerto Rico where electric exclusion has been effective (e.g., Pringle and Blake 1994; Pringle et al. 1999). Shrimps and *Sicydium* at

site U4 were consistently excluded by electricity (E. Greathouse, personal observation). At site U5, tadpoles included size classes that are smaller than organisms (native shrimps and fishes) known to be effectively excluded by the fence chargers we used. Thus, U5 observations were conducted on (1) control hoops, (2) electric hoops while electricity was on, and (3) electric hoops after electricity was turned off. At site U5, electricity excluded shrimps, reduced abundances of tadpoles > 1.5 cm, and had no effect on tadpoles < 1.5 cm (Greathouse 2005). *Sicydium* did not occur at site U5 (Greathouse 2005).

Shrimp addition experiments

At the two dammed sites (Greathouse 2005 site codes: D6, D7), we conducted enclosure experiments in areas within still-water pools, adding shrimps (*Xiphocaris*, *Atya* and *Macrobrachium*) to boulder/ bedrock areas (~1.5 m^2) enclosed by nylon block nets (mesh size 0.635 cm). Block nets blocked the vertical water column, but left the natural stream substrate within the enclosed area intact. We used cobbles to "seal" the nets to the stream bottom, and the tops of nets were tied to bank vegetation or stretched taut using stabilizing rocks on the bank such that the tops of the nets were at least 10 cm above the water surface. Numbers added were based on densities observed at undammed site U4 (45 per m^2). We also sampled control areas where shrimps were not added. Physical habitat (i.e., water depth, water velocity, canopy cover) was similar between shrimp and no shrimp treatments within and between sites, and in comparison to undammed experiment sites (E. Greathouse, personal observation). Experimental duration was short to minimize the possibility of storms washing out block nets. At site D6, we established three replicates of each treatment over four pools on 7 March 2003. Nine days after adding shrimps, we Loeb sampled, and we sampled macroinvertebrates and CBOM using the semi-quantitative benthic block net method (Greathouse and Pringle 2005). At site D7, we again established three replicates of each treatment over four pools on 7 June 2003. However, for sampling on days 4 (Loebs) and 7 (Loebs, macroinvertebrates, and CBOM), we also took advantage of our having accidentally released extra shrimps in a small pool and an area in a nearby pool unaffected by shrimps and included these as a fourth replicate. We placed a wooden hoop template in each treatment and control area in order to conduct macroconsumer observations using the same methods described for electric exclusion hoops.

Observations showed that treatments were effective, resulting in treatments with high shrimp densities (Greathouse 2005). Prior to statistical analyses, we averaged the repeated measures of parameters from Loeb sampling over days 4 and 7 to obtain a single value for each D7 replicate (Gotelli and Ellison 2004). Day 0 Loeb sampling showed that treatment and control areas did not differ in chlorophyll *a*, FBOM, and FBIM prior to adding shrimps (*P* values > 0.24, one-way ANOVAs).

Scale analyses

We compared responses in the experiments and the whole-stream perturbation using an approach modified from Kohler and Wiley (1997). For each response variable, we calculated:

1. Small-scale effect size (SES) = $-\ln(N_{\text{shrimp}}/N_{\text{noshrimp}})$
2. Large-scale effect size (LES) = $-\ln(N_{\text{u}}/N_{\text{d}})$

N_{shrimp} and N_{noshrimp} are mean values of response variables in treatments and controls where shrimp had access (N_{shrimp}) and treatments and controls where shrimp lacked access (N_{noshrimp}). N_{u} and N_{d} are the mean values of the response variables across the ten undammed sites (N_{u}) and seven dammed sites (N_{d}) surveyed by Greathouse et al. (2006). We then used linear regression to examine whether small- and large-scale effect sizes were correlated. A 1:1 correlation indicates a correspondence between the directions and magnitudes of effects in the small- and large-scale perturbations. We conducted separate regressions on seven measures of benthic resources (chlorophyll *a*, FBOM, FBIM, CBOM, C, N, C:N) and 13 categories of nondecapod invertebrate biomasses (total biomass and biomasses of the most common nondecapod invertebrate taxa, and an "other" category of the remaining uncommon taxa) using calculations of small-scale effect sizes from (1) undammed exclusion experiments only, (2) dammed addition experiments only, (3) all small-scale experiments combined (see Appendix 2 in Electronic Supplementary Material for description of calculations). Overall patterns and conclusions did not change when we repeated these regressions after excluding variables (chlorophyll *a*, FBOM, total biomass) that represent similar ecological components (i.e., carbon and nitrogen are sub-components of fine benthic organic matter; parts of the carbon and nitrogen are from chlorophyll *a*; and total biomass is the sum of biomasses of common invertebrate taxa and "other" invertebrates); thus, we only report full regressions.

Results

In each of the small-scale experiments, shrimp grazing consistently caused dramatic alterations of the benthos and epilithon (Appendices 1, 2 in Electronic Supplimentary Material). Rocks in unelectrified controls were grazed "clean" by shrimps, such that levels of algae, FBOM, FBIM, C, N, and nondecapod invertebrates were consistently low. In contrast, electric exclusion of high densities of shrimps caused large increases in these response variables (see Appendix 1b and c). Likewise, shrimp addition above large dams caused almost complete clearing of high levels of benthic resources and nondecapod invertebrates (see Appendix 1d and e). In "shrimp added" treatments, shrimps actively grazed the fine material and algae off of the rocks, creating "clean" patches that were gradually enlarged over the course of each experiment (E. Greathouse, personal observation). In contrast, "no shrimp added" controls had consistently high levels of algae, FBOM, FBIM, C, N, and nondecapods. The small-scale experiments did not alter CBOM or C:N levels (Fig. 1).

Differences between shrimp and no shrimp treatments of small-scale experiments are remarkably similar to differences between dammed and undammed sites visually (Appendix 1) and in terms of magnitude (Figs. 1, 2). Rocks in dammed and undammed survey pools consistently appeared like those in Appendix 1b and d, and undammed electric and "shrimp added" replicates consistently appeared like those in Appendix 1c and e. The magnitudes of effects show a strong 1:1 correlation for benthic resources for undammed exclusions only (LES $= 0.15 + 1.1 \cdot$ SES; $F_{1,5} = 42.4$, $P = 0.0013$, $r^2 = 0.89$), dammed additions only (LES $= 0.18 + 0.91 \cdot$ SES; $F_{1,5} = 75.3$, $P = 0.0003$, $r^2 = 0.94$), and all small-scale experiments combined (LES $= -0.12 + 1.1 \cdot$ SES; $F_{1,5} = 220.0$, $P < 0.0001$, $r^2 = 0.98$; Fig. 2). For nondecapod invertebrates, correlations are close to a 1:1 relationship. Slopes are generally consistent with a 1:1 relationship; however, regression intercepts are all approximately one, not zero (Fig. 2). Invertebrate correlations were also weaker (i.e., with lower r^2) than were benthic resource correlations for undammed exclusions only (LES $= 1.21 + 0.82 \cdot$ SES; $F_{1,10} = 4.3$, $P = 0.06$, $r^2 = 0.30$), dammed additions only (LES $= 1.06 + 0.98 \cdot$ SES; $F_{1,9} = 4.4$, $P = 0.06$, $r^2 = 0.33$), and all small-scale experiments combined (LES $= 1.18 + 0.91 \cdot$ SES; $F_{1,11} = 5.5$, $P = 0.039$, $r^2 = 0.33$). Small-scale effect size was not calculated for one invertebrate taxon in the undammed exclusions and two taxa in the dammed additions because of zero values in the no shrimp treatments (Fig. 2,
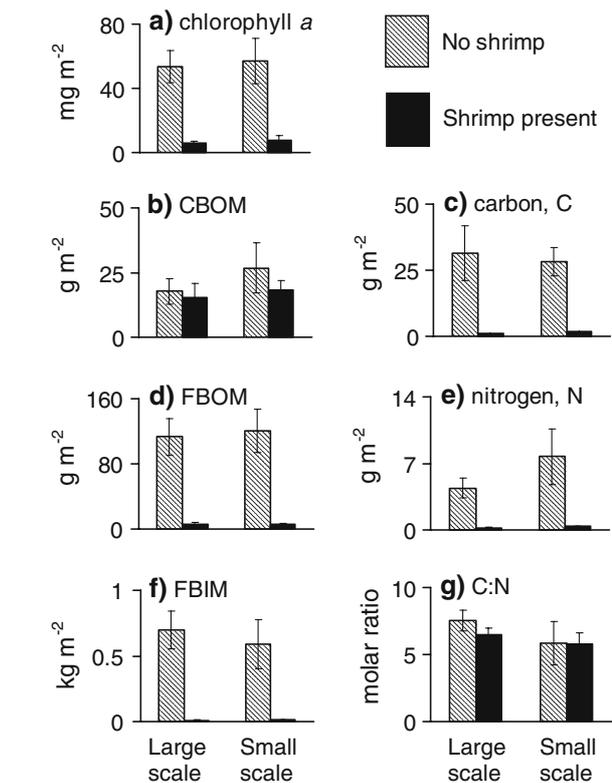
Fig. 1 Benthic resources (means ± 1 SE) in the large-scale perturbations in comparison to small-scale experiments with no shrimp (*shaded bars*) or with shrimp present (*solid bars*). The first two bars in each panel represent large-scale perturbations—sites above large dams (no shrimp) and sites with no large dams (shrimps present) observed in the survey described by Greathouse et al. (2006). Benthic resources observed are **a** chlorophyll *a*, **b** coarse benthic organic matter (CBOM), **c** carbon (C), **d** fine benthic organic matter (FBOM), **e** nitrogen (N), **f** fine benthic inorganic matter (FBIM), and **g** C:N

Appendix 2), but the directions of effects for these taxa are generally consistent with large-scale patterns.

Discussion

Our study provides a tropical example of extrapolation across vastly different spatial and temporal scales of food web perturbation. Arena sizes and durations of experimental treatments were ~0.25 m^2 and 25–27 days (electric treatments) and ~1.5 m^2 and 7–9 days ("shrimp added" treatments). In contrast, the perturbation of shrimp removal upstream from dams represents an "arena size" of ~2–20 km of stream length and a duration of 30–90 years. We observed a high correspondence of shrimp effects across scales for abiotic (fine inorganic sediments) and biotic factors (of at least three trophic levels: basal resources of algae and
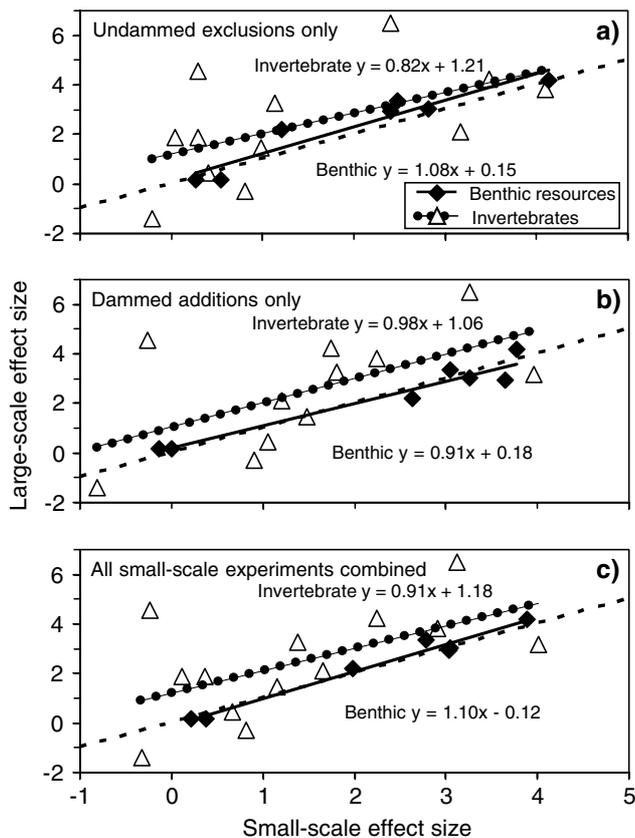
Fig. 2 Effect sizes in **a** undammed exclusions only, **b** dammed additions only, and **c** small-scale experiments combined vs. the large-scale perturbation for seven measures of benthic resources (chlorophyll *a*, FBOM, FBIM, CBOM, C, N, and C:N; *diamonds*) and 13 categories of nondecapod invertebrates (*triangles*). In each panel, *dashed lines* represent a perfect correspondence of small- and large-scale effects with slopes of one and intercepts at the origin. *Dotted lines* are for the regressions of invertebrate data only. *Solid lines* are for the regressions of benthic resource data only

detritus, herbivorous and detritivorous invertebrates, and predatory invertebrates). Our regression analyses indicate that small-scale experiments predicted the absolute magnitude of large-scale effects for benthic resources (regressions closely approximated a 1:1 line). For nondecapod invertebrates, small-scale experiments predicted the relative magnitudes of large-scale effects although they underestimated absolute magnitudes (regressions approximated a 1:1 line with an elevated intercept). To our knowledge, all other multiscale experimental research on consumer effects has been conducted in temperate regions, and studies generally examine only directions, not magnitudes, of effects.

We expected to find that small-scale experiments greatly underestimate effects when larger scales are involved, particularly for nondecapod invertebrates. Animal populations often require time and large areas in order to respond to changes in their environment.

Typical field experiments may be too small in scale and too short in duration for invertebrates, especially rare invertebrates, to respond to treatments (Kohler and Wiley 1997). The match between our small and large scales for nondecapod invertebrates is better than we expected. However, the r^2 of the correlations between small- and large-scale effect sizes is lower when invertebrates are analyzed separately, and most invertebrate data points fell above the 1:1 lines of perfect correspondence across scales. This finding indicates that the predictive power of small-scale experiments is not as high for invertebrates as it is for benthic resources.

Two other stream studies empirically examine the predictive capabilities of small-scale experiments in terms of magnitudes of effects. Similar to our study, both examine effects of strongly interacting, numerically-dominant, grazing stream invertebrates. In Colorado (USA), microcosm experiments underestimated the effects on algae of a whole-reach experiment (Taylor et al. 2002). In Michigan (USA), small-scale experiments predicted effects on algae, but substantially underestimated most effects on invertebrates on the large scale (Kohler and Wiley 1997). As in our study, the Michigan study used correlation of effect sizes in order to compare small-scale manipulations with replicated whole-stream perturbations. Although Kohler and Wiley (1997) observed congruence between the small and large scales for algae as ash-free dry mass (AFDM), their regression of effect sizes was not significant, data points showed no consistent pattern, and 13 of the 17 data points were above the 1:1 line of large- and small-scale correspondence.

A likely explanation for the differences in the predictive abilities of these experiments is that in the previous stream studies, experiments were in riffles, where rates of invertebrate movements and exchange processes are high. In contrast, we ran experiments in pools, where, during base flows, water velocities are near zero and nondecapod invertebrates have very low movement rates (Buzby 1998). Small-scale experiments in riffles are likely to function as highly open systems, where behavioral processes are more important (Cooper et al. 1990). However, in still-water pools, small-scale experiments are likely to function as less open systems, where demographic processes are more important. Likewise, large-scale perturbations, like pools, are likely to function as less open systems dominated by demographic processes (Englund 1997; Englund et al. 2001). Thus, in riffle studies, increasing the experimental scale (i.e., increasing the size of the perturbed area around the sampling location, Kemp et al. 2001) will be likely to cause a switch in the dominant processes (behavioral vs. demographic) affecting the

sampling location. Similar studies focusing on pools will be more likely to show no change in the processes dominating in the small vs. large scale (c.f., scale dependence of prey exchange in different stream habitats, Englund 1999; Englund et al. 2001; Englund and Hambäck 2004; also see Peckarsky et al. 1997). Because we did not conduct small-scale experiments in riffles, we cannot make firm conclusions about their predictive capability in this habitat. However, because we did examine riffles in the large-scale perturbation (Greathouse et al. 2006), we can conclude that any effects of experimental scale would not have been of the same nature as those observed by Kohler and Wiley (1997) or Taylor et al. (2002). On the large scale, our work showed no effects in riffles, whereas the aforementioned studies showed strong effects.

Differences between results in our warm-water systems in Puerto Rico vs. those in many cold-temperate studies (e.g., Gardner et al. 2001) might also be explained by differences between experimental grains/extents and natural scales (sensu Kemp et al. 2001). Small-scale experiments in warm-water systems may be more likely to predict large-scale effects because their experimental extents may be more easily matched to natural scales of response variables. For example, the life cycles of warm-water stream insects are generally multivoltine. Some taxa display life cycles as short as 1 week (Huryn and Wallace 2000). Thus, our 1- to 4-week experiments may encompass one or more generations of several insect taxa, meaning that the natural temporal scales of their population-level responses may be similar to the temporal extents of our experiments. In contrast, cold-temperate regions often require experimental durations upward of 10 months in order to span one or two insect generations (Kohler and Wiley 1997).

The frequency of flash flood disturbances in aseasonal tropical streams (e.g.,approximately one every 4–8 weeks in Puerto Rico) may also facilitate a match between the temporal scales of manipulations and the natural temporal scales of response variables. Depending on flood magnitude and antecedent conditions, floods can result in epilithic scouring, which may or may not be followed by deposition of fine organic and inorganic materials. Thus, above dams, floods can result in algal, FBOM, and FBIM levels that are temporarily as low as those that result from shrimp grazing in undammed streams (Greathouse 2005). During intervening periods of base flow, epilithon in sites above dams may generally be in a successional state that is similar to successional trajectories in electric exclusion treatments. Likewise, at sites without large dams, floods can result in temporary deposition of fine

materials, which shrimps are capable of removing rapidly after return to base flow (Pringle et al. 1999), similar to their rapid removal of epilithic materials in shrimp addition experiments in this study. Thus, small-scale experiments may be more likely to predict effects of large-scale perturbations in both tropical and temperate systems with frequent disturbances that reset the system. In contrast, systems with stable hydrologic regimes, such as the groundwater-dominated streams studied by Kohler and Wiley (1997), may show poor extrapolation because response variables are reset at intervals that are longer than lengths of typical small-scale experiments.

Another potential explanation for the predictive ability of our experiments is our use of experimental arenas that were open to the natural dynamics of their surroundings except for the intended treatment differences (e.g., macroconsumers). Because of their openness, the electric exclusions and the shrimp addition experiments were unaffected by typical mesocosm artifacts, which may have been a factor limiting extrapolation in the Colorado stream (Taylor et al. 2002). The electric exclusion technique avoids mesocosm/cage artifacts such as altered water velocity, dissolved oxygen, sedimentation rates, and insect movements (Pringle et al. 1999). Tests for the direct effects of electricity on sedimentation and nondecapod invertebrates (Pringle and Blake 1994) and algae (Brown et al. 2000) also reveal no artifacts of electricity. Likewise, in shrimp addition experiments, the sizes of the block net mesh and the netted areas were relatively large in order to avoid typical cage artifacts (e.g., mesh size was large relative to sizes of insects; placement of coarse-mesh block nets in still-water pools resulted in no artifacts of altered flow and sedimentation rates; E. Greathouse, personal observation).

Similar open-arena experiments in Michigan resulted in strong scale effects (Kohler and Wiley 1997). A potential explanation for this is that our experiments consisted of a combination of exclosure and enclosure methods, while experiments in Michigan used exclusions only. Exclosures and enclosures might show differences in predictive ability because use of open arenas results in treatments that are small patches surrounded by dissimilar conditions, while controls are embedded in a matrix of similar conditions. Combining exclosure and enclosure methods results in controls that represent both levels of the experimental factor. For example, undammed unelectrified controls served as ambient shrimp density treatments, and "no shrimp added" controls served as "no shrimp" treatments. As a result, ambient-shrimp-density controls at the two undammed sites were embedded in a large matrix (i.e.,

many kilometers of stream habitat) containing ambient shrimp densities. Likewise, "no shrimp added" controls at the two dammed sites were embedded in a large matrix devoid of shrimps. Thus, in our set of small-scale experiments, there effectively were large-scale, long-term treatments for both levels of the main factor (shrimp present vs. no shrimp present). However, in our study, this was not of great importance—there were only small differences among the predictive abilities of: electric exclusions alone, shrimp additions alone, and the combination of exclusion and addition experiments together. In contrast, in other systems, exclusion and addition experiments may cause different results (Wiseman et al. 1993). Thus, combining small-scale experiments and detailed surveys of field conditions may result in opportunities for creatively embedding small-scale experiments within large-scale conditions that represent all levels of the treatment. Such opportunities may enhance extrapolation across scales.

An eventual goal of scale research is to be able to extrapolate results from small-scale experiments with confidence, even when large-scale experiments and perturbations are lacking. Development of scaling rules, theory, and models to pursue this goal will require considerable empirical data on both successful and unsuccessful cross-scale comparisons across a wide variety of ecosystems, biomes, and habitats. However, to date, few studies have empirically examined the predictive capabilities of small-scale experiments in terms of magnitudes of effects (Englund and Cooper 2003). Our study adds critical data comparing both the directions and magnitudes of effects in small-scale experiments with large-scale perturbations in tropical, warm-water streams.

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