

# Effects of littoral habitat complexity and sunfish composition on fish production

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**Abstract** – Habitat complexity is a key driver of food web dynamics because physical structure dictates resource availability to a community. Changes in fish diversity can also alter trophic interactions and energy pathways in food webs. Few studies have examined the direct, indirect, and interactive effects of biodiversity and habitat complexity on fish production. We explored the effects of habitat complexity (simulated vegetation), sunfish diversity (intra- vs. inter-specific sunfish), and their interaction using a mesocosm experiment. Total fish production was examined across two levels of habitat complexity (low: 161 strands  $m^{-2}$  and high: 714 strands  $m^{-2}$ ) and two sunfish diversity treatments: bluegill only (*Lepomis macrochirus*) and bluegill, redear sunfish (*Lepomis microlophus*), and green sunfish (*Lepomis cyanellus*) combination. We also measured changes in total phosphorus, phytoplankton, periphyton, and invertebrates to explain patterns in fish production. Bluegill and total fish production were unaffected by the sunfish treatments. Habitat complexity had a large influence on food web structure by shifting primary productivity from pelagic to a more littoral pathway in the high habitat treatments. Periphyton was higher with dense vegetation, leading to reductions in total phosphorus, phytoplankton, cladoceran abundance and fish biomass. In tanks with low vegetation, bluegill exhibited increased growth. Habitat complexity can alter energy flow through food webs ultimately influencing higher trophic levels. The lack of an effect of sunfish diversity on fish production does not imply that conserving biodiversity is unimportant; rather, we suggest that understanding the context in which biodiversity is important to food web dynamics is critical to conservation planning.

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## Introduction

Habitat complexity (Gonzalez & Chanton 2002; Eriksson et al. 2006; Warfe & Barmuta 2006) and biodiversity (Hooper et al. 2005) are both strong controlling factors of ecosystem function. Understanding the influence of habitat complexity on ecosystem function is critical due to the alteration of littoral zones from changes in human land use (Christensen et al. 1996; Sass et al. 2006; Roth et al. 2007; Grabowski et al. 2008). Similarly, an increasing number of research studies are exploring the ability of biodiversity to govern ecosystem function that is driven by a

need to understand the consequences of the dramatic changes in biodiversity from species loss and invasion (Naeem et al. 2002; Worm & Duffy 2003; Cardinale et al. 2006). Although many examples demonstrate the effects of these two factors independently, habitat complexity and biodiversity are not mutually exclusive (Srivastava 2006; Warfe & Barmuta 2006). In aquatic ecosystems, interactions are likely as habitat complexity can influence processes that are associated with biodiversity mechanisms, such as foraging efficiency, nutrient pathways, primary productivity and resource partitioning (Eriksson et al. 2006; Smokorowski et al. 2006). Limited data exists exploring their

interactive effects (Srivastava 2006; Warfe & Barnuta 2006; Replansky & Bell 2009), thus a simultaneous test of the effects of habitat complexity and fish diversity will expand our understanding of food webs by considering the potential interaction of these key factors.

Alterations to habitat complexity can affect ecosystem function by directly influencing species involved in ecosystem processes or indirectly influencing other trophic levels (Srivastava 2006). Habitat complexity directly affects food webs by altering predator–prey interactions and changing the physical environment (Carpenter & Lodge 1986; Wahl 1995; Denno et al. 2002; Grabowski et al. 2008). Increasing complexity provides more refuge for prey thereby decreasing predator capture efficiency (Crowder & Cooper 1982; Savino & Stein 1982; Scheffer 1999; Manatunge et al. 2000; Ruetz et al. 2006; Genkai-Kato 2007). By creating a refuge, habitat complexity can indirectly affect food webs by facilitating top–down control of primary producers from increased consumer density (Jeppesen et al. 1997; Stephen et al. 2004; Genkai-Kato 2007). The abundance and distribution of aquatic plants, for example, can affect primary production by creating more available substrate for periphyton colonisation that reduces resources available to phytoplankton, decreases light availability by shading, and increasing sedimentation rates of phytoplankton cells (Carpenter & Lodge 1986; Vis et al. 2006; Declerck et al. 2007). Other direct effects from increasing habitat complexity can be to reduce the number of encounters among competitive species by creating more niche space (Srivastava 2006). Overall, habitat complexity controls energy transfer through food webs by direct and indirect influences on top–down and bottom–up pathways and may impact the strength of the link between littoral and pelagic habitats especially in small aquatic systems (Declerck et al. 2007).

Biodiversity has been suggested as a key determinant of ecosystem function (Hooper et al. 2005); however, questions remain about the relevance of current biodiversity studies to natural systems, because most studies have been conducted on primary producers (Gessner et al. 2004; Covich et al. 2004; Ives et al. 2005; Bruno et al. 2006). Exploring the governing influence of fish diversity allows consumer effects to be evaluated as a determinant of ecosystem properties. The central tenet of a biodiversity effect is a difference between intra- and inter-specific interactions differentially altering ecosystem properties. For instance, systems with higher biodiversity of consumers, and thus more efficient use of resources by inter-specific interactions, are expected to be more productive than monocultures (Hooper et al. 2005; Cardinale et al. 2006; Srivastava 2006; Hargrave 2006). Fish assemblages are a highly diverse compo-

nent of aquatic systems and comparing intra- and inter-specific interactions provides a valuable first step in exploring the effects of consumer diversity.

Sunfishes (*Lepomis* spp.) are a good model to test the importance of habitat complexity and differences between intra- and inter-specific interactions on ecosystem properties, because they are ecologically diverse and are influenced by habitat complexity (Werner & Hall 1976, 1979; Mittelbach 1981). In sympatry, bluegill (*L. macrochirus*), pumpkinseed (*L. gibbosus*), and green sunfish (*L. cyanellus*) partition resources with bluegill utilising open water, green sunfish concentrating in vegetation, and pumpkinseed foraging on benthic resources (Werner & Hall 1976, 1977, 1979; Mittelbach 1981). The different resources utilised from this niche separation are suited to the morphology and behaviour of each species (Werner & Hall 1977; Mittelbach 1981) and could lead to resource complementarity between sunfish species resulting in increased total fish production (Giller et al. 2004; Downing 2005; Kahmen et al. 2006; Yachi & Loreau 2007). Bluegill have been found to have strong effects on food webs relative to fishless controls (Nowlin & Drenner 2000), thus we used bluegill as a focal species to test intra- versus inter-specific interactions with other sunfish species. Previous studies have used additive designs to test differences in effects of sunfish communities (e.g., Werner & Hall 1976); however, additive designs are limited in that changes in species are confounded with changes in total amounts of fish by holding intraspecific interactions constant. A substitution design allows comparisons of the relative importance of intra- versus inter-specific interactions by holding biomass constant while manipulating species combinations (Goldberg & Scheiner 1993; Griffen 2006). Constant biomass between combinations of fish also provides a robust comparison of consumer effects on lower trophic levels (Bruno & O'Connor 2005).

Using a substitution design, we explore the effects of intra- versus inter-specific interactions of sunfish (sunfish diversity: bluegill vs. bluegill, redear sunfish (*L. microlophus*), and green sunfish) across two levels of habitat complexity (low and high stem density). We hypothesise that total fish biomass will increase from single to combined species due to resource partitioning among sunfish. Thus, we expected higher total fish biomass with mixed sunfish species relative to bluegills only. Increasing habitat complexity (low to high stem density) is expected to have strong bottom–up effects by increasing substrate for periphyton growth (Carpenter & Lodge 1986), providing a larger refuge for invertebrates (Scheffer 1999), and increasing the amount of niche space. Total fish production should be increased by higher habitat complexity due to more resource space to be partitioned among species.

Finally, a positive interaction between sunfish diversity and habitat complexity would increase total fish production, because higher habitat complexity will create more resource space and enhance the complementarity effect of the sunfish species. For bluegills, there are opposing outcomes as habitat complexity may reduce access to zooplankton prey, but should also produce benefits by reducing intraspecific interactions. To explore these predictions, we manipulate sunfish species and habitat complexity in experimental mesocosms.

## Methods

### Experimental design

The study was conducted in 16 polyethylene tanks (1.5 m diameter  $\times$  0.60 m) located at the Sam Parr Biological Station, Kinmundy, IL, USA. To maintain natural water temperatures in the tanks, all tanks were floated on the surface of a 0.4-ha pond and secured in place using four metal stakes. Before the experiment (01 August), two sediment trays (35  $\times$  22  $\times$  4.5 cm) were added to opposite sides of each tank. Each tray contained 5 kg wet mass of pond sediment and associated benthic invertebrates (composition density) that were collected from the littoral zone of the pond. Simulated vegetation was added to each tray at two density levels (low: 161 stems  $m^{-2}$ ; high: 714 stems  $m^{-2}$ ). We used artificial plants to examine the physical structure of plants independent of other effects, such as competition for nutrients (Declercq et al. 2007). Each simulated plant stem was constructed of 0.6 cm diameter polypropylene rope 35 cm in length (Ostrand et al. 2004). Rope sections were secured to wire mesh (1  $\times$  1 cm) and placed in the bottom of each tray prior to adding sediments. Tanks were then filled with pond water to a depth of 0.45 m (800 l) and the experiment began 1 week later.

On 08 August, we added locally collected sunfish to each tank at two treatment levels. Fish treatments were replicated in a substitution design that held initial fish biomass constant to reflect natural conditions where increasing diversity reduces population densities of individual species through interspecific interactions (Bruno & O'Connor 2005). Fish were young-of-year and averaged  $2.77 \pm 0.13$  g (mean  $\pm$  1 SE) in wet weight. The first fish treatment involved only bluegills: we added three, similar-sized bluegill to four low and four high stem density habitat tanks. For the second fish treatment, we added one similar size individual of each sunfish species (bluegill, redear sunfish and green sunfish) to four low and four high habitat tanks. In total, we had four treatments: Low Habitat:Bluegill Only (LB); High Habitat:Bluegill Only (HB); Low Habitat:Mixed Sunfish (LM); High Habitat:Mixed Sunfish

(HM). Similar total biomass was added to each tank across treatments (mean  $\pm$  1 SE: LB  $8.2 \pm 0.48$ , HB  $8.1 \pm 0.71$ , LM  $8.1 \pm 0.46$ , HM  $8.9 \pm 0.42$ ) to conserve initial fish biomass (ANOVA,  $P = 0.63$ ). Treatments isolating all individual species and combinations were not logistically feasible across habitat treatments. We focused on bluegill for the single species treatment, because it is the mostly widely distributed sunfish species. Tanks were covered with bird-proof nets (6 mm mesh). Some fish of each species were reared in separate (nonexperimental) tanks and used to replace mortalities with equally sized individuals. Mortalities were very few overall ( $N = 4$ ) and randomly distributed across treatments and time. One low habitat, mixed sunfish (LM) tank was lost during the experiment leaving only three replicates of this treatment.

### Data collection

Experiments lasted 8 weeks during which we measured total phosphorus in the water column, chlorophyll *a* in the water column, and zooplankton weekly in each tank beginning 10 August. Three water samples were collected from the entire water column using an integrated tube sampler (60 mm diameter) and then transferred to a mixing bucket. Chlorophyll *a* was obtained by filtering 100 ml of water onto glass fibre filters (Whatman GF/F), extracting chlorophyll in 90% acetone for 24 h, and then measuring fluorescence using a fluorometer (Turner Design, model TD700, Sunnyvale, CA, USA). Total phosphorus in the water column was also measured from the integrated water sample (250 ml) within 1 h of collection using the colourimetric molybdenum blue ascorbic acid method with a persulphate digestion (Wetzel & Likens 1991). Zooplankton were sampled weekly using the integrated tube sampler; on each sampling date, three samples were obtained from each tank. Each of the three samples was collected from different locations in each tank (centre, edge and edge of vegetation), combined in a mixing bucket, filtered through a 150- $\mu$ m mesh net, and then rinsed into sample containers and preserved with 5% Lugol's solution (Wallace & Snell 2001). In the laboratory, samples were adjusted to constant volume (100 ml) and sub-sampled in 1-ml aliquots. Zooplankton were identified under a dissecting scope into taxonomic groups of *Daphnia*, other cladocerans, calanoids, cyclopoids, and nauplii and whole subsamples were counted until 200 organisms of each of the most common taxa were enumerated (Welker et al. 1994). We focused on cladocerans in subsequent analyses because they are a primary prey of sunfish (Werner & Hall 1977, 1979) and the most efficient grazers in our system (Brooks & Dodson 1965).

Benthic macroinvertebrates were sampled from each sediment tray at the midpoint (18 September)

and end (14 October) of the experiment using an acrylic core sampler. Six samples (total area = 46 cm<sup>2</sup>) were obtained from each tank (three per tray) and combined in a sieve bucket (250 μm). Samples were sieved of fine sediments, rinsed into 500 ml sample containers and preserved with a solution of 0.1% rose Bengal stain and 90% ethanol. In the laboratory, all benthic macroinvertebrates were identified and enumerated. Taxa-specific body dimensions were measured for at least 30 individuals from each sample and used as input in length–weight regression equations to estimate individual dry mass (Dumont et al. 1975; Smock 1980; Benke et al. 1999). Mean individual dry mass was then extrapolated by area to obtain estimates for each tank and sampling date combination. At the end of the experiment, we also collected periphyton from each tank; one stem was randomly removed from each tray (2 stems per tank), and each stem placed in a 500-ml beaker and carefully scraped of periphyton using a small brush and rinse bottle containing distilled water (Fisher Scientific, Optima W7–4, Pittsburg, PA, USA). Additional distilled water was then added to each beaker to bring the total volume to 250 ml and the sample was thoroughly mixed. From the mixed sample, 35 ml was extracted, placed in a 50-ml culture tube, and total phosphorus was measured as outlined above (Wetzel & Likens 1991). Similarly, 100 ml was extracted from the mixed samples, filtered onto glass fibre filters (Whatman GF/F) and analyzed for chlorophyll *a* biomass as outlined earlier. Total phosphorus (μg P per stem) and chlorophyll *a* biomass (μg chlorophyll *a* per stem) measured for each stem was then averaged for each tank. In addition, on the final day, lengths (total length, nearest 0.1 mm) and body masses (nearest 0.1 g wet mass) were determined for individual fish.

Statistical analysis

We tested for effects of habitat and sunfish treatments on water column chlorophyll *a*, water column total

phosphorus, and cladoceran density with repeated measures ANOVA (Proc Mixed, SAS 8.2; SAS Institute Inc., Cary, NC, USA). Water column chlorophyll *a* and cladoceran density were log-transformed to satisfy the homogeneity of variance assumption. Sampling date, habitat level, and sunfish were fixed effects and we tested for all interactions. Following a significant sunfish, habitat, or interaction term, we tested for a difference among treatments with a least squares means multiple comparison test with Tukey–Kramer adjustment. When a significant time interaction was detected, we used the SLICE option in SAS to partition the effect of time and then tested for treatment effects (Littell et al. 2002).

We tested for effects of habitat complexity and sunfish diversity on periphyton biomass (chlorophyll *a*), periphyton total phosphorus, benthic invertebrate biomass, relative change in total fish biomass (mean by tank), and bluegill productivity (g·day<sup>-1</sup>) using a two-way ANOVA. When main effects or interaction terms were significant, we performed least squares means multiple comparisons with Tukey–Kramer adjustment. For the mixed sunfish tanks we also tested for fish species and habitat complexity effects on species-specific relative change in biomass. Benthic invertebrate biomass was log-transformed to satisfy the homogeneity of variance assumption of ANOVA.

Results

Total phosphorus in the water column differed between habitat treatments (*P* = 0.002) and time (*P* < 0.0001), with an interaction detected between time and sunfish treatments (*P* = 0.0003; Table 1). Low habitat treatments generally had higher levels of total phosphorus than high habitat treatments. Low habitat treatments initially increased in total phosphorus until about the fourth week, when phosphorus in both low and high habitat treatments began to decrease (Fig. 1A). No interaction was detected between the habitat and sunfish treatments (Table 1). Within

Table 1. Repeated measures anova on water column total phosphorus (μg P·l<sup>-1</sup>), water column chlorophyll *a* (μg·l<sup>-1</sup>), and cladoceran density (#·l<sup>-1</sup>) in mesocosm experiments examining the effects of two habitat treatments (low and high stem density), two sunfish treatments (bluegill only and mixed sunfish) and their interactions.

Effect	Phosphorus				Chlorophyll <i>a</i>				Cladoceran density			
	NDF	DDF	<i>F</i>	<i>P</i>	NDF	DDF	<i>F</i>	<i>P</i>	NDF	DDF	<i>F</i>	<i>P</i>
Time	8	87	5.11	<0.0001	8	84	13.37	<0.0001	7	77	2.62	0.02
Habitat	1	11	16.67	0.002	1	11	3.65	0.08	1	11	22.19	0.0006
Sunfish	1	11	0.05	0.82	1	11	1.84	0.20	1	11	0.09	0.77
Time × Habitat	8	87	0.48	0.86	8	84	0.40	0.92	7	77	1.79	0.10
Time × Sunfish	8	87	3.23	0.003	8	84	1.47	0.18	7	77	0.51	0.82
Habitat × Sunfish	1	11	0.00	0.97	1	11	0.41	0.54	1	11	0.42	0.53
Time × Habitat × Sunfish	8	87	0.78	0.62	8	84	0.74	0.66	7	77	0.97	0.46

Numerator degrees of freedom (NDF), denominator degrees of freedom (DDF), *F* statistics, and *P*-values are presented for each analysis.

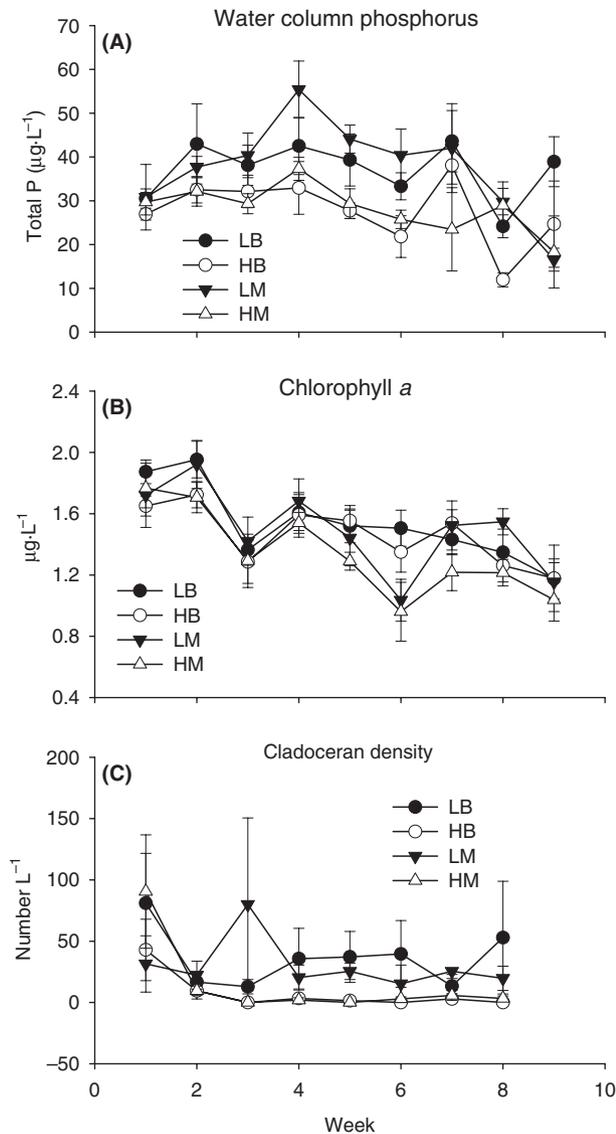


Fig. 1. Weekly mean ( $\pm 1$  SE) for (A) water column total phosphorus ( $\mu\text{g P}\cdot\text{L}^{-1}$ ), (B) chlorophyll *a* ( $\mu\text{g}\cdot\text{L}^{-1}$ ) and (C) cladoceran density ( $\text{L}^{-1}$ ) over the 8 week experiment across treatments [Low Habitat:Bluegill Only (LB); High Habitat:Bluegill Only (HB); Low Habitat:Mixed Sunfish (LM); High Habitat:Mixed Sunfish (HM)].

habitat levels, total phosphorus also did not differ between bluegill only and mixed sunfish treatments. A significant interaction term with time indicated that the sunfish treatments affected total phosphorus differently through time (Table 1, Fig. 1A). The least squares multiple comparison test (SLICE option) showed that total phosphorus in both bluegill only and mixed sunfish treatments changed temporally (both  $P < 0.01$ ). Despite a significant effect of time, the sunfish treatments had no effect and there was no consistent pattern in the changing relationship between sunfish treatments across weeks.

Similar to phosphorus, water column chlorophyll *a* declined through time in all treatments (Table 1);

however, the habitat treatment was significant at  $P = 0.08$ . The low habitat treatments had higher levels of chlorophyll *a* relative to the high habitat treatments (Fig. 1B). No differences were detected between the bluegill only and mixed sunfish treatments for chlorophyll *a* and no interactions were detected among time, habitat, and sunfish treatments (Table 1).

Periphyton biomass (chlorophyll *a*) and total phosphorus content in the periphyton was primarily affected by the habitat treatments (Table 2). Periphyton biomass, as indexed by chlorophyll *a*, was significantly higher in high habitat treatment than the low habitat treatments (Fig. 2A) and no differences in chlorophyll *a* were found between the bluegill only and mixed sunfish treatments within each habitat treatment (Tukey test,  $P > 0.1$ ). Similarly, periphyton phosphorus was significantly higher in high habitat treatment than the low habitat treatments (Fig. 2B), but no differences were detected between sunfish treatments within each habitat treatment (Tukey test,  $P > 0.1$ ). Overall, periphyton levels (both biomass and total phosphorus) were significantly higher in high habitat treatments than the low habitat treatments (Fig. 2A,B).

Sunfish composition had no effect on potential prey resources, whereas habitat treatments influenced zooplankton density but not benthic macroinvertebrate biomass. Cladoceran zooplankton included individuals from Daphniidae, Chydoridae and Sididae families. Significant time and habitat effects were found for cladoceran density (Table 1). Following an initial decline by the second week, the low habitat treatments had increased densities of cladocerans relative to the high habitat treatments (Fig. 1C). No effects of sunfish treatments or interactions were detected for cladocerans (Table 1). Benthic macroinvertebrates primarily consisted of Anisoptera, Caenidae, Ceratopogonidae, Chaoboridae, Chironomidae, Culicidae, Ephemerae, Hydrophilidae, Hirudinea, Oligochaeta, Trichoptera, and Zygoptera. There was a higher richness of benthic macroinvertebrates than zooplankton, but no effect of the habitat or sunfish treatments were detected for any of the specific benthic taxa. Furthermore, total benthic macroinvertebrate biomass did not vary with habitat treatments, sunfish treatments, or interactions between treatments at either the midpoint or end of the experiment (Table 2; Fig. 2C).

Differences between high and low habitat treatments also drove the patterns observed in total fish production. Gain in total fish biomass was significantly affected by habitat treatments (Table 2), with biomass gains in low habitat treatments greater than in the high habitat treatments (Fig. 3A). Differences between the bluegill only and mixed sunfish treatments had no influence on total fish biomass and no interaction was detected between sunfish and habitat

Table 2. Two-way anova examining the effects of two habitat treatments (low and high stem density), two sunfish treatments (bluegill only and mixed sunfish), and their interactions on the final values for periphyton total phosphorus ( $\mu\text{g P per tank}$ ), periphyton biomass (chlorophyll *a*  $\mu\text{g per tank}$ ), benthic macroinvertebrate biomass ( $\text{g}\cdot\text{m}^{-2}$ ), fish growth (final  $\text{g}/\text{start g}$ ) and bluegill productivity ( $\text{g}\cdot\text{day}^{-1}$ ) in mesocosm experiments.

Effect	Periphyton biomass			Periphyton Phosphorus			Benthic invertebrate biomass			Percent change in fish mass			Bluegill production ( $\text{g}\cdot\text{day}^{-1}$ )		
	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P
Habitat	1	20.47	0.001	1	94.92	<0.0001	1	1.74	0.22	1	20.71	0.0008	1	8.01	0.02
Sunfish	1	0.23	0.64	1	0.51	0.49	1	0.21	0.66	1	2.32	0.16	1	0	0.96
Habitat $\times$ Sunfish	1	0.24	0.63	1	2.89	0.12	1	2.6	0.14	1	0.64	0.44	1	0.64	0.58

treatments (Table 2). Examining only bluegill productivity ( $\text{g}\cdot\text{day}^{-1}$ ), there was a significant effect from the habitat treatments ( $P = 0.02$ ), no difference between bluegill only and mixed sunfish treatments ( $P = 0.96$ ), and no interaction between habitat and sunfish treatments ( $P = 0.58$ ; Table 2). Bluegill productivity was higher in the low stem density treatments than in the high density treatments.

Within the mixed sunfish treatments, species-specific changes in biomass were affected by both habitat ( $P = 0.0001$ ) and individual species ( $P = 0.02$ ), with no interaction between factors. Higher biomass was found in the low habitat treatment, but the strength of the pattern differed among species. Green sunfish had significantly higher growth in the low than the high habitat treatments ( $P = 0.003$ ; Fig. 3B). Similarly, growth of bluegill in the low habitat treatment was marginally higher than in the high habitat treatment within the mixed sunfish treatments ( $P = 0.08$ ; Fig. 3B). In contrast, no effect of habitat was found on growth in redear sunfish (Fig. 3B). Comparing across species, green sunfish grew more than redear sunfish within the low habitat treatments ( $P = 0.05$ ), whereas bluegill were intermediate and not different from other species ( $P > 0.42$ ). No differences were detected between species within the high habitat treatments (all  $P > 0.90$ ).

**Discussion**

We found significant changes in food web structure through time largely mediated by differences in habitat complexity. Habitat complexity can affect ecosystem function by directly affecting the species performing the function or indirectly via linkages with other trophic levels (Srivastava 2006). A strong influence of habitat complexity on ecosystem processes is thought to result from both increased surface area and more niche space (Carpenter & Lodge 1986; Rennie & Jackson 2005; Smokorowski et al. 2006; Srivastava 2006; Declerck et al. 2007). Specifically, increasing littoral habitat complexity in aquatic systems can alter energy pathways through the food web by providing more substrate for periphyton (Smokorowski et al. 2006; Vadeboncoeur et al. 2006), consequently redi-

recting and reducing nutrient availability to pelagic components of food webs (Wetzel 2001; Rennie & Jackson 2005; Vis et al. 2006; Lauster et al. 2006; Declerck et al. 2007). A bottom-up effect from increased habitat complexity was the primary driver in our system. The high stem density treatment provided four times the amount of substrate for periphyton colonisation. Increased periphyton likely reduced the phosphorus available to phytoplankton, indirectly reducing cladoceran density, and ultimately lowering total fish production. In general, increasing habitat complexity created a strong bottom-up effect, shifting the resource base of the food web from the open water to benthic pathways. Invertebrates that consume periphyton and could redirect energy towards fish productivity from benthic primary production were low in our system. The presence of an algavore, either invertebrate or vertebrate, may reconnect the benthic pathway and have important interactions with the changes observed from habitat complexity. Researchers have often overlooked the potential for benthic primary production (Vadeboncoeur et al. 2002); yet benthic primary production can comprise a substantial portion of the whole-lake primary production. The amount of contribution may depend on factors such as substrate, lake area, morphometry, and trophic state (Vander Zanden et al. 2006). The high contribution and ability to alter energy pathways through the food web suggest more research directed at benthic primary production will be insightful.

We expected that habitat complexity would have a direct positive effect on zooplankton and benthic invertebrate communities. Higher abundance and richness in the invertebrate community often results from increasing habitat complexity due to the greater heterogeneity in resources (i.e., niche space) and more refuge space from predators (Gerrish & Bristow 1979; Crowder & Cooper 1982; Schmude et al. 1998; Rennie & Jackson 2005; Ruetz et al. 2006). Contrary to these predictions, we found no response of macroinvertebrates, and cladoceran biomass actually decreased with increased habitat complexity. Plant architecture has recently been found to influence periphyton, macroinvertebrate communities, and predator foraging (Cheruvilil et al. 2002; Valley &

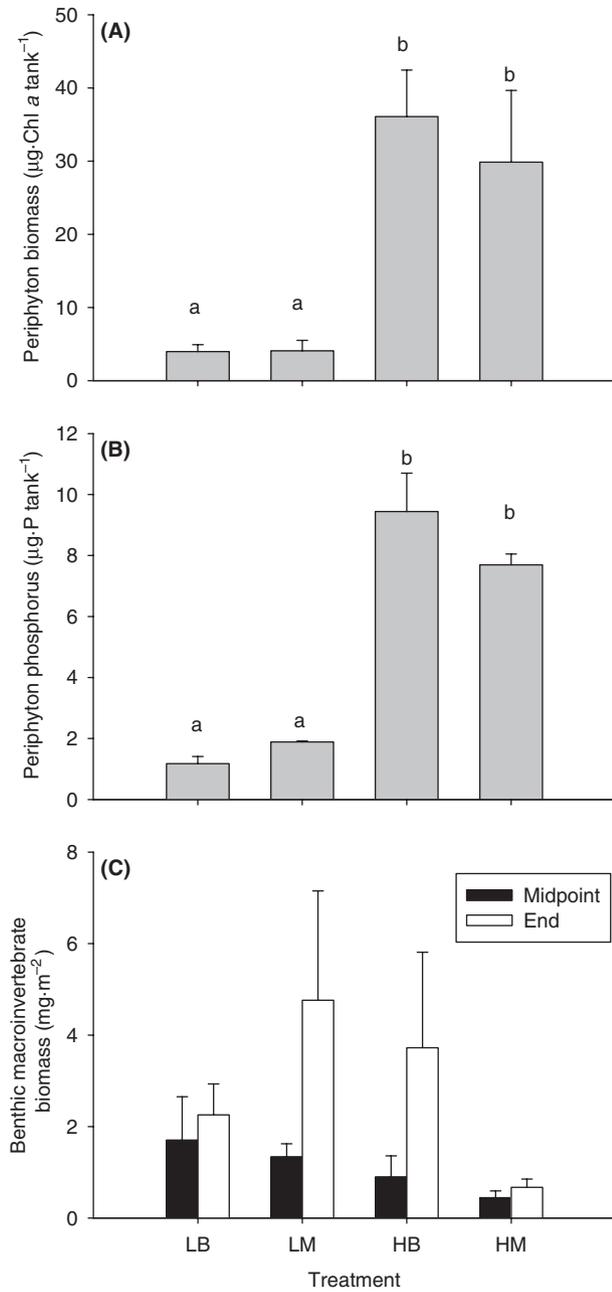


Fig. 2. Mean (±1 SE) across treatments in mesocosms for (A) total phosphorus in the periphyton (µg P per tank) at the end of the experiment, (B) periphyton biomass (chlorophyll a µg per tank) at the end of the experiment, and (C) benthic macroinvertebrate biomass (g·m<sup>-2</sup>) at the midpoint (18 September) and end (14 October) of the experiment across all treatments [Low Habitat:Bluegill Only (LB); High Habitat:Bluegill Only (HB); Low Habitat:Mixed Sunfish (LM); High Habitat:Mixed Sunfish (HM)]. For periphyton in A and B, different lowercase letters indicate significant differences between treatment combinations (Tukey test,  $P < 0.10$ ).

Bremigan 2002; Warfe & Barmuta 2006). Incorporating differences in plant architecture is likely a key next step to understanding the effect of habitat complexity and biodiversity on food web structure.

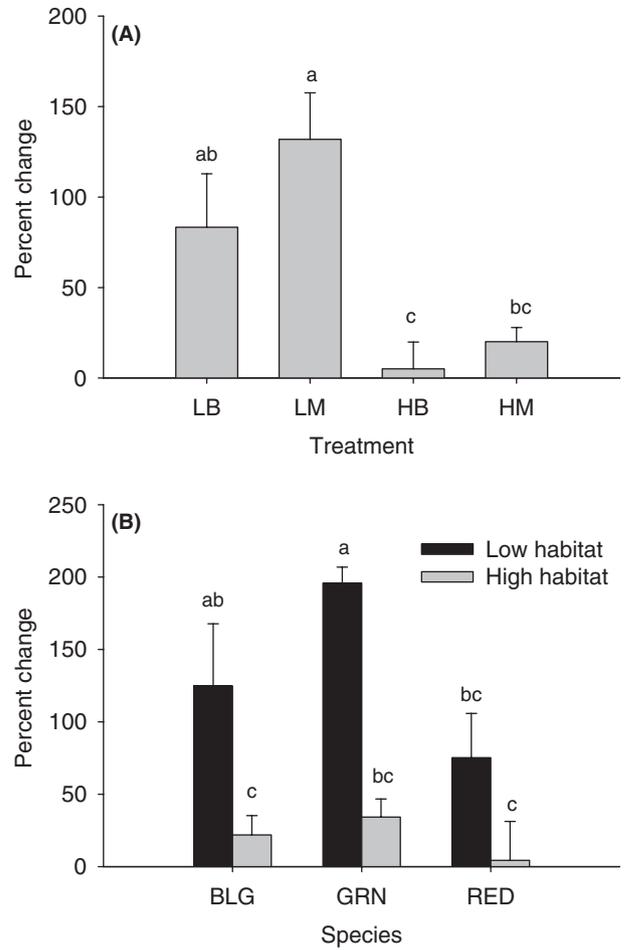


Fig. 3. Percent change (±1 SE) in (A) mean biomass of fish in mesocosms at the end of the experiment across all treatments [Low Habitat:Bluegill Only (LB); High Habitat:Bluegill Only (HB); Low Habitat:Mixed Sunfish (LM); High Habitat:Mixed Sunfish (HM)] and in (B) mean biomass of fish by species (BLG, bluegill; GRN, green sunfish; RED, redear sunfish) in mixed sunfish treatments at the end of experiment across habitat treatments of low and high stem density. Different lowercase letters indicate significant differences between treatment combinations (Tukey test,  $P < 0.05$ ).

Differences between intra- and inter-specific interactions of sunfish did not have a strong, direct influence on either total fish production or other components of the food web. Total fish and bluegill production did not increase between the bluegill only and the mixed sunfish treatments as predicted by an increase in diversity. Based on previous studies with other taxa and emerging paradigms regarding the influence of biodiversity (Hooper et al. 2005; Naeem 2002), resource partitioning among sunfish species was expected to increase overall production. Although overall production was not affected by the sunfish treatments, species-specific responses did differ within the mixed sunfish treatments. Bluegill profited from more open water in the low habitat treatments. Green sunfish used higher habitat complexity most efficiently

as expected (Werner & Hall 1976), but this species was also more productive in the low habitat treatment. Differences among species were only apparent in the low habitat treatments. Because sunfish species partition resources when combined (Werner & Hall 1976), we also expected that differences between bluegill only and mixed sunfish would transform food web structure through trophic interactions. Changes within sunfish treatments were not observed, suggesting differences in traits and interactions among species were not strong controls of food web structure. The lack of an effect on ecosystem function does not imply conserving biodiversity is unimportant in aquatic systems, instead, we suggest understanding the context in which biodiversity is important to ecosystem function is critical.

Lack of strong effects on ecosystem function due to intra- or inter-specific interactions may be due to several factors. Currently, debate exists about whether increasing species or functional diversity will have greater effects on ecosystem function (Petchey et al. 2004; Hooper et al. 2005; Srivastava 2006). All species we used are from the same genus, found in similar habitats, and occupy similar trophic levels. Thus, we focused on species diversity rather than functional diversity. In addition, trait differences between sunfish species that have been found to influence community dynamics (e.g., Werner & Hall 1976) may be insufficient to detect in ecosystem processes. Specifically, sunfish have been found to partition resources, but differences may not be functionally large enough to elicit changes in food web structure at the size range used in our experiment. If sunfish were more specialised consumers, theories on linkages between biodiversity ecosystem functions would predict a stronger effect (Ives et al. 2005). The simplicity of our experimental food webs may have forced more overlap in species niches than is found in natural lakes or in the experimental ponds where resource partitioning was first suggested for sunfish species (Werner & Hall 1976). Furthermore, although not directly tested in our experimental design, resource limitation may affect patterns when comparing intra- to inter-specific interactions (Weis et al. 2007). Although logistically difficult, future research should explore these relationships in natural systems and expand the range in species richness. In addition to top-down foraging effects, fish diversity can influence food webs through effects on nutrient patterns and bottom-up pathways. Fish can shift benthic-derived energy via excretion as soluble reactive phosphorus into open water (Okun et al. 2005; Hargrave 2006). A bottom-up effect could move throughout the food web increasing productivity at all trophic levels. Either we did not find top-down or bottom-up influences from changing sunfish treatments on food web structure, or

these processes may have offset one another in effects on energy flow. Finally, individual effects of each sunfish species could not be addressed without replicating individual species treatments and as a result we could not determine if the probability of a given species being present and driving ecosystem function (sampling effect; Hooper et al. 2005) was an important process (Loreau & Hector 2001; Giller et al. 2004). Bluegill may be a dominant species within our species pool as it is the most efficient at using open water habitat and may not be significantly influenced by structural complexity. Dominant species can make differences from resource complementarity inconsequential to ecosystem function (Hooper et al. 2005). Without replicating individual species treatments, we are also unable to test if the direction of effect was different between sunfish species. Future studies need to account for individual species (Loreau & Hector 2001) and use experimental designs that incorporate both an additive and substitution approach to both hold intra-specific interactions constant and maintain the amount of total fish across species compositions (Finke & Denno 2004; Bruno & O'Connor 2005). Examining other species combinations, especially all individual species, would allow further exploration of the effects of biodiversity and explicitly determine the mechanisms (sampling effect and resource complementarity) for fish diversity to govern ecosystem function.

A positive, synergistic interaction was expected between increasing sunfish diversity and habitat complexity on total fish production as well as other components of the food web. By creating more resource space, we thought higher habitat complexity might accentuate the effect of resource partitioning between sunfish species. The only interaction we found was between habitat and sunfish diversity effects on periphyton. Specifically, differences between low and high habitat was not as strong for periphyton in the mixed sunfish treatment relative to the bluegill only treatment. Mixed sunfish species may have reduced habitat effects by exploiting more resource space and moving nutrients within the food web. All species had reduced growth in the high habitat treatments relative to the low habitat treatments indicating increased periphyton altered energy pathways away from fish production. Specifically for bluegill, resource availability was reduced, yet within the high habitat treatment bluegill growth in mixed sunfish treatments was higher than in the bluegill only treatments. Thus, bluegill appear to benefit from the change from intra- to inter-specific interactions when resources are low. Overall, habitat complexity exerted a stronger bottom-up influence than top-down effects from fish diversity by redirecting energy flow through the food web.

Despite the pelagic zone being the focus of most limnological studies (Wetzel 2001; Vadeboncoeur et al. 2002; Vander Zanden et al. 2006), benthic pathways are fundamental to understanding aquatic ecosystems. The lack of focus has resulted in a poor understanding of the interactions across habitats; however, some work on cross-habitat energy linkages has shown how strongly they can influence trophic dynamics (Beklioglu & Moss 1996; Vander Zanden et al. 2005). Our study demonstrates how linkages or disconnects between littoral and pelagic habitats can have implications for overall food web structure and alter the importance of other factors, such as biodiversity. Littoral complexity dominated ecosystem processes through bottom-up effects via periphyton that indirectly affected phytoplankton and ultimately influenced fish production. The strength of the links between littoral and pelagic habitats likely varies with the size of the lentic system, in particular, the littoral-pelagic ratio (Genkai-Kato 2007). Scaling the questions we have addressed to larger systems will be useful for meeting restoration and conservation objectives.

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