Development and Use of an Ecopath Model to Explore Effects of Habitat Restoration Projects on Florida Lake Fish Communities

FINAL REPORT

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Executive Summary

Resource management agencies and researchers have struggled to assess how changes in habitat composition and abundance will influence fish communities and fisheries. This research need pertains to both freshwater (lakes and rivers) and marine environments, and has been an increasingly important focus of fisheries management agencies over the last decade. Regarding freshwater systems, there is a need to identify plant types and abundances that foster high diversity and provide valuable habitat to sport fish. Ecosystem models offer the potential to explore how restoration projects that alter habitat quality and quantity will influence fish communities and fisheries.

The Florida Fish and Wildlife Conservation Commission (FWC) has conducted some of the largest lake habitat restoration projects in the world over the past two decades. In an effort to mediate effects of channelization and stabilized water levels on large lakes, and for aquatic plant management purposes, the FWC has used lake drawdowns and muck removals to improve littoral habitat. Drawdown and muck removal projects open areas to access by anglers and homeowners, but the benefits to fisheries have varied (e.g., Moyer et al. 2005; Allen et al. 2002) and impacts to lake-wide fish communities have not been measured. A key need for lake habitat restoration projects is the ability to set realistic objectives and measure the system's responses relative to those objectives.

The goal of this project was to develop a spatially explicit ecosystem model for a generalized large Florida lake and use the model to explore how changes in habitat composition could influence fish community and sport fish abundance. Our objectives were to: 1) to analyze existing databases in Florida and evaluate the precision of estimates of fish biomass, density, community composition (e.g., total richness, density, and biomass of species groups) and

evaluate how they vary with aquatic plant species composition and abundance, 2) to develop an Ecopath model using input parameters from the historical data and other Florida studies, and 3) use the model to explore how changes in aquatic plant coverage and composition were predicted to influence fish community composition and abundance.

Historical block net data showed few clear relationships between fish functional group biomasses and habitat types (Chapter 1). Within habitats, we found few significant correlations between individual fish functional group biomasses and vegetation density metrics. Sampling area (i.e., block net size) influenced fish functional group biomass and habitat evaluations, thus illustrating the importance of considering gear size-selectivity and sampling timing for describing biomass-habitat relationships. For example, estimated biomass per area for largemouth bass was much higher in 0.08 ha block nets than in 0.01 ha block nets because the smaller block nets did not effectively capture fish > 200 mm total length and sampling was done in fall. Differences in size-structure among habitats were detected for some sport fish groups with implications for ecosystem model structure and assignment of preferred habitats. Power analyses indicated that block net data precision would limit the ability to evaluate effectiveness of habitat restoration projects using density metrics. Results from historical data analysis (e.g., fish biomass per area, sport fish habitat use) were used to develop an ecosystem model that incorporated habitat influences on fish communities.

Our ecosystem model was structured to represent a large Florida eutrophic lake and was built using Ecopath with Ecosim/Ecospace software (Chapter 2). Functional groups within the model were linked through diet composition data and population dynamics parameter inputs. The model was balanced (i.e., functional group production exceeded total mortality) and then used in Ecosim/Ecospace to predict how habitat manipulations (i.e., littoral habitat restoration

via tussock control) would influence fish community composition and fisheries. In Ecosim, we modeled three habitat restoration scenarios: 1) "no control", 2) a "10-year control" that reduced tussock biomass every 10 years by inducing high "mortality" on the tussock functional group, and 3) a "combined control" scenario that reduced tussock biomass every 10 years and used maintenance controls (e.g., herbicides) between 10-year removal periods. Ecosim predicted that our "combined control" scenario provided the largest long-term habitat restoration benefits for sport fish abundance and the fisheries they support. In Ecospace, we simulated a littoral habitat restoration project that reduced lake-wide tussock coverage from 30% to 15%. Ecospace predicted positive benefits to sport fish and fisheries following the restoration simulation and highlighted the importance of edge effects, spatial design of habitat restoration projects, and sampling design of restoration evaluations.

This project provided an assessment of historical block net data for determining fish community and habitat relationships and an ecological modeling tool for investigating potential habitat restoration projects in Florida lakes. Major conclusions were that 1) variability in block net catches largely limited the ability to detect fish community and habitat relationships and precision of ecosystem model biomass inputs, and 2) ecosystem models provide an exploratory tool for deriving expectations of habitat restorations and exposing trade-offs of alternative habitat management options. The project also identified important research needs for refining hypotheses that structured ecosystem interactions and for designing and evaluating habitat restoration projects. For example, the ecosystem model indicated that edge effects could potentially offset negative effects of poor quality habitat resulting from tussocks. Thus, the value and necessity of habitat restoration projects may depend on the potential beneficial qualities of edge habitats. This highlighted a research need to quantify the relative value of edge habitats for

fishes, and explore how the value changes with the proximity and size of high quality habitat. There is also a need to explore effects of restoration efforts on other taxa such as wading birds and reptiles. Ecosystem models such as those developed in this study can provide a framework for a science-based approach to setting goals and evaluating success of lake restoration projects in Florida.

Chapter 1: Analysis of Historical Block net Data to Describe Fish-Habitat Relationships and Sampling Precision

In this chapter we evaluated historical block net data sets that were collected within quantified habitats to expose fish community and habitat relationships.   Our objectives were to: analyze existing databases in Florida and evaluate the precision of estimates of fish biomass, density, community composition (e.g., total richness, density and biomass of species guilds) and how they vary with aquatic plant species composition and abundance. We also evaluated block net sampling efficiency for determining differences in fish community metrics.

Methods

Data

We compiled historical rotenone fish data sets collected using three gear types from eight lakes that also had vegetation metrics collected within the sampling areas (Table 1-1). Data collected from differing habitats and sampling areas were treated with 5% rotenone at $\geq$ 2ppm. Lake Okeechobee data were collected using 0.08 ha block nets and 0.004 ha Wegener rings from 1989 to 1991 from stratified vegetation types (Bull et al. 1991). Block nets were 3.4 m deep with 3 mm bar mesh and were used to target fish $\geq$ 6 cm total length (TL). Wegener rings were placed within block nets and were used to collect fish $<$ 6 cm TL. Fish were measured for total length and grouped into two cm groupings and weighed to the nearest gram. Vegetation strata for Lake Okeechobee samples included: bulrush *Scirpus californicus*, eelgrass *Vallisneria americana.*, emergent grass (e.g., *Paspilidium geminatum*), hydrilla *Hydrilla verticulata*, Mexican waterlily (e.g., *Nymphea mexicana*), Illinois pondweed *Potamogeton illinoensis*, and

spikerush *Eleocharis celluslosa* (Bull et al. 1991). Vegetation biomass and stem densities were estimated within each block net to provide an index of aquatic vegetation density, however vegetation metrics were not measured in 1989. We also used data collected from open water sites using 0.08 ha block nets at Orange Lake during 1990, 1992, and 1998. We used Orange Lake block net data because it allowed for evaluation of fish community biomass in open water sites from a eutrophic lake that had a vastly vegetated littoral zone (Estes and Myers 1996), whereas there were no open water samples collected with 0.08 ha nets at Lake Okeechobee. We also used data from six eutrophic lakes distributed across Florida's latitudinal gradient (i.e., Lakes Harris, Istokpoga, Monroe, Okeechobee, Seminole, and Talquin) using 0.01 ha block nets across multiple vegetated habitats (Rogers and Allen 2005). Vegetation biomass and total percent area covered (PAC) were estimated within each 0.01 ha block net. Vegetation biomass was estimated by removing all aquatic vegetation within three randomly located 0.25 m^2 quadrats and weighing the removed vegetation. Total PAC was estimated visually within the block net and percent composition of PAC by submergent, emergent, and floating plant types was estimated. Lastly, we used rotenone data collected in 0.01 ha block nets at Lakes Istokpoga and Kissimmee during 2005 and 2006 (Bunch et al. 2008). Vegetation biomass and total PAC were estimated with the same methods used by Rogers and Allen (2005).

We classified catches by habitat types based on the dominant plant type found in each sampling unit (i.e., block net or Wegener ring) to allow for comparisons among habitats and fish communities across the data sets. Plants were considered dominant if they comprised greater than 65% of the total stem density, biomass, or PAC in a sampling area. Classification of habitat types by dominant plant was required for informing the ecosystem model's structure in Chapter 2.

Analysis

We estimated biomass per hectare for species groupings (hereafter referred to as functional groups) to facilitate development of the ecosystem model in Chapter 2. Species were grouped based on foraging ecology (i.e., functional groups) as suggested for Ecopath with Ecosim models (Christensen et al. 2000), however species of importance to fisheries (e.g., largemouth bass and black crappie) were treated as their own functional group to facilitate exploration of habitat enhancement affects on popular sport fish. Functional groups for the ecosystem model and their species composition are listed in Table 1-2.

Catch data were corrected for recovery rate and standardized to catch per area (i.e., biomass per hectare) to establish relationships between aquatic vegetation types and fish communities. We estimated recovery rates to correct observed block net catches using different methods depending on the gear type and data collection method. Recovery rates for 0.08 ha block nets and 0.004 ha Wegener rings were estimated using a Bayesian hierarchical model developed for depletion experiments, which allowed for site specific estimates of capture probability (Dorazio et al. 2005). We built a Bayesian hierarchical model using the WinBUGS program (Lunn et al. 2000) for common habitat types in the data set (i.e., bulrush, eelgrass, emergent grass, hydrilla, water lily, pondweed, spikerush, and open water). The Bayesian hierarchical model allowed for estimation of abundance and capture probability from spatially distinct subpopulations (i.e., block net locations) and for estimation of the posterior distribution of capture probability across all sites within a vegetation type (Dorazio et al. 2005). Thus, we were able to use the posterior distributions of capture probability for each habitat type to correct observed catches for incomplete recovery. We assumed that abundances across sites followed a multinomial-Poisson mixture distribution and that the capture probability hyperparameter for all

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vegetation types followed a beta distribution (Dorazio et al. 2005). We treated three-day pick up

data as individual depletion events, thus allowing estimates of capture probability for each net

within a vegetation type. We applied the "empirical Bayes" estimates of the mean capture

probability and standard deviation for each vegetation type to correct catches from 0.08 ha block

nets and 0.004 ha Wegener rings. We incorporated variability in capture probabilities by

dividing observed catches by a random deviate drawn from a beta distribution with a mean equal

to the "empirical Bayes" capture probability mean and standard deviation for each vegetation

type. We used a bootstrap procedure to resample (i.e., 1,000 resamples) recovery rate corrected

catches to create the expected distribution of functional group biomasses (i.e., kg/ha) for each

vegetation type. We used correlation analysis to evaluate habitat-specific relationships between

vegetation stem density and site-specific capture probability estimates for the Lake Okeechobee

0.08 ha block net data. Correlation analysis could not be done for Wegener ring data because

Wegener rings were set within the 0.08 nets and did not have individual vegetation metrics

measured.

Three day pick-up data were not available for 0.01 block net data, thus recovery rates for

vegetation types were estimated using mark-recapture data from previous studies. Mark-

recapture experiments were conducted at Lake Dora in 1980 (Wicker and Johnson 1987) and at

Lakes Istokpoga and Kissimmee in 2006 and 2007 (Bunch et al. 2008). Recovery rates at Lake

Dora were estimated by releasing marked hatchery raised fingerling largemouth bass into block

nets prior to rotenone application. Recovery rates at Lakes Kissimmee and Istokpoga were

estimated by releasing fathead minnows *Pimepheles promelas*, which did not occur in the

habitats sampled at those lakes, into block nets prior to rotenone application. Recovery rate was

estimated as the proportion of fish recovered relative to the total number released into each net.

We used recovery rates from commonly sampled habitat types (i.e., submersed (e.g., eelgrass) and emergent (e.g., bulrush) vegetation, emergent grass (e.g., *Panicum spp.*), mixed communities (i.e., no dominant plant type could be identified), and open water). Recovery rates from each vegetation type were resampled (i.e., 1,000 times) to create the expected distribution for recovery rates for each habitat. Relationships between 0.01 ha block net capture probability and plant density could not be evaluated because although we had dominant habitat type data for nets, we did not have plant density or biomass estimates from most sites. To evaluate functional group biomass and habitat relationships for specific habitats, we applied recovery rate to estimates from sites within common habitat types (e.g., recovery rate estimate for emergent vegetation was applied to catches from both cattail and bulrush). We corrected 0.01 block net catches for each habitat type by drawing a random number from a beta distribution with a mean and standard deviation that followed the bootstrap results for each vegetation category. We resampled (i.e., 1,000 resamples) recovery rate corrected catches to create the expected distribution of functional group biomasses (i.e., kg/ha) for each vegetation type sampled with 0.01 ha block nets.

We used recovery rate corrected catches from each net to evaluate relationships between functional group biomass and vegetation abundance (i.e., stem density or vegetation biomass $(kg/0.25m^2)$) using linear regression. Functional group biomass and vegetation abundance metrics were $\log_e$-transformed to normalize residuals. We evaluated relationships between functional group biomass and vegetation abundance to determine if vegetation abundance affects functional group distributions, to provide insight into habitat quality habitat quality for developing the ecosystem model, and to facilitate predictions of fish community effects following habitat modifications.

We used data from 0.08 ha block nets and Wegener rings set within those block nets to compare species richness across habitat types. We totaled the number of species captured at each site for each vegetation type to determine species richness and resampled those counts for each habitat type 1000 times to create the expected distribution of species richness by habitat. We used 95% confidence intervals from the resampling procedure to determine if species richness varied by habitat.

We evaluated relationships between sport fish (i.e., largemouth bass, bluegill, redear sunfish, and black crappie) size composition and vegetation type to determine if abundance of adults and subadults for those groups differed among vegetation types. Adult sizes were determined by evaluating length frequencies from 0.08 ha block net catches from Lake Okeechobee. We only used 0.08 ha block net data for these evaluations to minimize selectivity against large individuals found with 0.01 ha block nets and Wegener rings. We used a general linear model using a LOGIT transformation to compare the ratio of adult biomass to total biomass for sport fish by habitat type (Neumann and Allen 2007). Multiple comparison tests with Tukey's modification for experimentwise error were used to separate ratios for models where habitat was a significant factor. Evaluating size structure and plant community relationships will facilitate the spatial structure of the ecosystem model and simulations of plant management effects on fish community size structure in our ecosystem model.

We evaluated the effectiveness of using 0.08 ha and 0.01 ha block nets to detect changes in sport fish biomass, species richness, and species diversity. We estimated the number of samples required and power associated with detecting 20%, 50%, and 80% biomass changes. Power was calculated using a non-central F distribution (Gerow 2007).   For species accumulation estimates with increased sample sizes, we used a jackknife procedure with random

data entry using the "Vegan" package (Oksanen et al. 2008) in R (R Development Core Team 2008). Evaluating the ability to detect biomass changes with these sampling gears is important for future attempts of validating the outputs of our ecosystem model and determining the usefulness of these gears as monitoring tools.

Results and Discussion

Posterior distributions of capture probability from hierarchical models showed few differences among habitat types. Capture probability for 0.08 ha block nets was lower in bulrush than in eelgrass, pondweed, and open water, but capture probability in bulrush did not differ from the other habitat types (Figure 1-1). Capture probability in hydrilla was marginally higher than in bulrush (95% credible intervals = 0.37 – 0.62, and 0.22 – 0.28, respectively). Thus, capture probability appeared higher in submerged vegetation and open water than in bulrush habitats. Vegetated habitats at Lake Okeechobee had high plant coverages (i.e., >85 %, Miller et al. 1990), and thus, lower capture probability in bulrush may have been due to decreased mobility and visual constraints of seeing floating fish relative to submerged vegetated habitats and open water. Capture probability estimates from hierarchical models for Wegener ring data showed similar trends to 0.08 ha block nets because capture probabilities were higher for submerged vegetation habitats than for bulrush and Mexican water lily (Figure 1-2). Capture probability estimates for 0.01 ha block nets using recovery rates of marked fish showed similar results to those using hierarchical modeling because capture probabilities in emergent (e.g., bulrush) and emergent grass (e.g., maidencane *Panicum hemitomon*) habitats were significantly lower than those in submerged vegetation and open water habitats (Figure 1-3).

Correcting for capture probability is critical for allowing data from multiple gears and habitat types to be comparable because of potentially differing gear size selectivity and habitat influences on recovery rates. Our capture probability estimates indicated that biomass estimates could be greatly underestimated using observed data, but the magnitude of measurement error depended on habitat types. Our estimates of capture probability were similar to other published estimates for block net data derived from capture-recapture data. Johnson et al. (1988) reported results from five studies where average recapture rates from mark-recapture ranged from 17% to 96%, and recovery rates from 0.08 block nets in littoral and open water habitats at Lakes Rowell and Lochloosa, Florida averaged 61% and 43%, respectively (M. Hoyer, University of Florida, unpublished data). Bayley and Austen (1990) found that area sampled negatively influenced recovery rates of marked fish in coves and ponds, however their sampling areas were larger (i.e., 0.09 – 5.09 ha) than the areas sampled in our analysis (i.e., 0.004 – 0.08 ha). Fish length also influenced recovery and was maximized between 150-200 mm (Bayley and Austen 1990); however recovery rates were not affected by species type. Other studies (e.g., DuRant 1980) have shown that capture probability can vary among species and may be an important consideration for correcting observed catches to estimate abundance. We could not account for species effects on recovery rates in our capture probability estimates because of data limitations (i.e., need more samples in each habitat), however hierarchical models could be developed for each functional group or common species if enough data were available. Furthermore, covariates such as length could be incorporated into the Bayesian hierarchical model to help explain factors that influence recovery rates. Our analysis is the first attempt we are aware of to use three-day pickup data as depletion events for estimating capture probabilities. Field tests of hierarchical model estimates relative to capture-recapture data are suggested in the future to

validate their results and determine if 3-d pickup data meet assumptions (e.g., population closure) required for application as depletion data.

Correlations between capture probability estimates and vegetation density were weak in most cases. Negative correlations between capture probabilities in 0.08 ha block nets and vegetation densities were found for bulrush and spikerush (Figure 1-4). Bayley and Austen (1990) reported that macrophyte coverage did not significantly contribute to their ability of explaining recovery rates from block nets, however they failed to describe the vegetation types or coverage levels in their sampling areas. We expected strong negative correlations between capture probability and vegetation biomass in submersed plant habitats due to fish getting tangled in vegetation, and thus, making them harder to detect. However, we did not find negative relationships between capture probability and submersed plant density and the range of capture probability estimates were similar across gears for this plant type.

We found few relationships between fish functional group biomasses and vegetation types, and patterns were not always consistent across gears. For example, bulrush supported higher biomass for some functional groups (e.g., largemouth bass) than other habitats sampled with 0.08 ha block nets, but those results were not supported for other gears (e.g., 0.01 ha block nets, Figure 1-5). Largemouth bass biomass estimates in 0.08 ha nets were extremely high and were likely overestimated because of the low capture probability estimate for bulrush. Largemouth bass biomass in 0.08 nets could have been overestimated if this species was recovered at a higher rate than other species relative to their true abundance. Overestimation could have also occurred if this species had higher vulnerability to rotenone than other species because their size distribution was comprised of larger fish relative to other functional groups. Despite the magnitude of our largemouth bass biomass estimate in bulrush, Bull et al. (1991)

reported high largemouth bass biomass in bulrush (242.4 kg/ha and 98.8 kg/ha at Lake

Okeechobee in 1989 and 1990) without correcting for recovery rate. Mexican water lily habitats

sampled with 0.08 ha nets generally had low sport fish biomass. Open-water habitats sampled

with 0.08 ha nets had low biomass for all groups except zoobenthivorous fish, which was

expected because this group contains shad and catfish species (Figure 1-5). Fewer differences

for functional group biomasses among habitats were found with 0.01 ha nets relative to the larger

block nets (Figure 1-6). Largemouth bass biomass in bulrush estimated from 0.01 ha nets was

significantly lower than in some habitats (e.g., cattail), whereas largemouth bass biomass

estimated from 0.08 ha nets was significantly higher in bulrush than in other habitats. The

magnitude of biomass estimates from 0.08 ha nets and 0.01 ha nets were often very different.

For example, largemouth bass biomass estimates from 0.08 and 0.01 ha block nets ranged from

2.0-427.2 kg/ha and 0.4-8.7 kg/ha, respectively. However, this result was not surprising given

the inherent size selectivity of the gears. Rogers and Allen (2005) reported that 0.01 ha block net

catches were minimal for fish greater than 150 mm total length, and thus, the biomass

differences between the two gears was probably influenced by gear selectivity. Our analyses

suggested that the ecosystem model should not depict large differences in functional group

biomasses across littoral habitat types.

Fewer functional group biomass and habitat relationships could be evaluated using

Wegener ring data than for block nets. Wegener ring data comparisons were limited because of

the gear's size selectivity and timing of sampling. Wegener rings are useful for sampling fish $\leq$

6 cm total length (Miller et al 1990), but our data were collected in the fall when age-0 fish of

some species likely had low catchability to this gear due to their total length (e.g., largemouth

bass) or were not using vegetated littoral habitats. Thus, only functional groups that contained

small fish in fall could be evaluated. Few differences were found in functional group biomass estimated from Wegener ring data among habitats, but generalists and prey functional groups generally had lower biomasses in submerged vegetation than in water lily habitats (Figure 1-7). However, zoobenthivorous fish had lower biomass in water lily habitats than in some other habitats (Figure 1-7).

The variability associated with block net catches limited our ability to detect biomass differences for fish functional groups among habitats, however we were able to identify some relationships between functional group biomass and vegetation density. The strongest relationship between functional group biomasses and plant density in 0.08 ha nets was positive for bluegill in hydrilla and negative for centrarchids in emergent grass habitats (Figure 1-8). The only strong relationship between functional group biomasses and plant densities from 0.01 ha nets was positive for predators in pondweed habitats ($r^2 = 0.67$, $P < 0.01$). Thus, we were unable to make broad conclusions about the quality of specific habitat for functional group biomasses. Community interactions (e.g., prey availability) likely determine habitat quality for functional groups and the ecosystem model should highlight dynamics that influence habitat use by functional groups.

We found no differences in species richness across habitat types sampled with 0.08 ha block nets. Mean species richness ranged from 12 to 17 species per block net, but 95% confidence intervals overlapped for all habitat types (Figure 1-9). Thus, no habitat type we evaluated appeared to facilitate higher fish community diversity than other habitat types in our analysis. In contrast to our results, Bunch et al. (2008) reported differing species richness across a range of emergent plant types, but they found no differences in species diversity across habitat types or coverage levels at Lakes Istokpoga and Kissimmee. Bunch et al.'s (2008) study targeted

high densities of emergent plants that were expected to exhibit habitat limitations for fish groups with differing stress (e.g., dissolved oxygen) tolerances, and thus, we were not surprised to find contrasting results to Bunch et al. (2008) in our study. Furthermore, habitats that may limit species diversity because of poor water quality (e.g., dissolved oxygen; see Moyer at al. 1995, Tugend and Allen 2004, Bunch et al. 2008) are difficult to sample with gears that sample large areas, and thus, data included in our analysis were rarely collected in poor habitats. We will use data exclusively from Bunch et al. (2008) in our ecosystem model to represent functional group densities in dense emergent macrophytes because these habitats were not well represented among the other data sources.

We found some differences in size composition among habitats for some sport fish functional groups. Adult and subadult size ranges for sport fish are shown in Figure 1-10. The proportion of biomass consisting of adults was similar for largemouth bass across habitats, but there were differences between bulrush and native submerged plants (i.e., pondweed and eelgrass, Tables 1-3 and 1-4). This indicated that largemouth bass biomasses in pondweeds and eelgrass consisted of more juveniles relative to largemouth bass biomass in bulrush. The proportion of biomass consisting of adult bluegills exhibited multiple differences across habitats (Tables 1-5 and 1-6). In general, the proportion of bluegill biomass that was adults was lowest in eelgrass and highest in bulrush. The proportion of redear sunfish biomass consisting of adults was significantly lower in eelgrass than in all other habitats and few other differences were found among habitats (Tables 1-7 and 1-8). Lastly, the proportion of black crappie biomass that were adults showed few differences across habitats and the absence of black crappie from block nets sampled in spikerush prevented that habitat from being included in the analysis. The proportion of black crappie biomass consisting of adults was lowest in hydrilla and this proportion was

significantly lower than the proportion found in bulrush (Tables 1-9 and 1-10). Size composition evaluations suggested that the ecosystem model should consider spatial distributions of sport fish adults and subadults, which may have influences on predator-prey interactions in dynamic simulations.

Block nets were efficient for determining species richness among habitats, but variability in block net catches limited the power of this gear to detect changes in total abundance within habitats. Species richness could be determined with fewer than 10-0.08ha block nets in almost all habitats (Figure 1-11). Power simulations suggested that 0.08 ha block nets would require less effort to determine large changes (i.e., > 50%) in species richness and diversity (i.e., Shannon-Weiner diversity) than total abundance within habitats (Figures 1-12, 1-13, and 1-14). High effort would be required to detect changes in functional group abundances within habitats using 0.08 ha block nets (APPENDIX I). This result suggested limitations to using block nets as a tool to validate ecosystem model outputs in the future.

Table 1-1. Blocknet data sources used to evaluate fish community- habitat relationships and biomass inputs for a large eutrophic Florida lake ecosystem model.

Data source	Years sampled	Lake	Sampling gear	Sampling unit area	Aquatic vegetation metric
FWC	1989-1991	Okeechobee	Block net	0.08 ha	stem density*
FWC	1989-1991	Okeechobee	Wegener ring	0.004 ha	stem density*
UF	2003-2004	Harris	Block net	0.01 ha	PAC, biomass
UF	2003-2004, 2006	Istokpoga	Block net	0.01 ha	PAC, biomass
UF	2003-2004	Monroe	Block net	0.01 ha	PAC, biomass
UF	2003-2004	Okeechobee	Block net	0.01 ha	PAC, biomass
UF	2003-2004	Seminole	Block net	0.01 ha	PAC, biomass
UF	2003-2004	Talquin	Block net	0.01 ha	PAC, biomass
UF	2005	Kissimmee	Block net	0.01 ha	PAC, biomass
FWC	1990-1998	Orange	Block net	0.08 ha	NA**

FWC = Florida Fish and Wildlife Conservation Commission, UF = University of Florida, PAC = Percent area covered,

* = vegetation metrics were not measured in 1989, ** = only open water samples were used.

Table 1-2. Species composition of functional groups for evaluating relationships between aquatic vegetation and fish communities and developing an ecosystem model for a large Florida eutrophic lake.

Functional group	Species composition	
Predators	bowfin	Amia calva
	chain pickerel	Esox niger
	Florida gar	Lepisosteus platyrhincus
	snook	Centropomis undecimalis
	ladyfish	Elops saurus
	longnose gar	Lepisosteus osseus
Largemouth bass	largemouth bass	Micropterus salmoides
Black crappie	black crappie	Pomoxis nigromaculatus
Bluegill	bluegill	Lepomis macrochirus
Centrarchid	bluegill	Lepomis macrochirus
	spotted sunfish	Lepomis punctatus
	redear sunfish	Lepomis microlophus
	dollar sunfish	Lepomis marginatus
	warmouth	Lepomis gulosus
	bluespotted sunfish	Enneacanthus gloriosus
	redbreast sunfish	Lepomis auritus
	Pygmy sunfish	Elassoma sp.
Prey	golden topminnow	Fundulus chrysotus
	mosquitofish	Gambusia sp.
	seminole killifish	Fundulus seminolis
	sailfin molly	Poecilia latipinna
	least killifish	Heterandria formosa
	bluefin killifish	Lucania goodei
	lined topminnow	Fundulus lineolatus
	rainwater killifish	Lucania parva
	russetfin topminnow	Fundulus escambiae
	flagfish	Jordanella floridae
Generalists	brook silverside	Labidesthes sicculus
	atlantic needlefish	Strongylura marina
	opposum pipefish	Microphis brachyurus
	pugnose minnow	Opsopoeodus emiliae
	sheepshead minnow	Cyprinodon variegatus
	striped mullet	Mugil cephalus
	golden shiner	Notemigonus crysoleucas
	taillight shiner	Notropis maculatus
	tidewater silverside	Menidia peninsulae
	coastal shiner	Notropis petersoni
Zoobenthivorous fish	swamp darter	Etheostoma fusiforme
	lake chubsucker	Erimyzon sucetta
	tadpole madtom	Noturus gyrinus
	threadfin shad	Dorosoma petenense
	gizzard shad	Dorosoma cepedianum
	clown goby	Microgobius gulosus
	channel catfish	Ictalurus punctatus
	brown bullhead	Ameiurus nebulosus
	blue tilapia	Tilapia aurea
	white catfish	Ameiurus catus
	yellow bullhead	Ameiurus natalis
	pirate perch	Aphredoderus sayanus
	hogchoker	Trinectes maculatus
	sailfin catfish	Pterygoplichthys multiradiatus
	naked goby	Gobiosoma bosc
	black acara	Cichlasoma bimaculatum
	Brown haplo	Hoplosternum littorale

Table 1-3. Proportion of total biomass comprised of adult largemouth bass by habitat

Habitat	Proportion of total biomass comprised of adult largemouth bass
Bulrush	0.65
Eelgrass	0.45
Emergent grass	0.62
Hydrilla	0.54
Water lily	0.55
Pondweed	0.39
Spikerush	0.84

Table 1-4. Analysis of Variance multiple comparison p-values for proportion of total biomass comprised of adult largemouth bass among habitats.

	Bulrush	Eelgrass	Emergent grass	Hydrilla	Water Lily	Pondweed	Spikerush
Bulrush		<.01	0.84	0.18	0.46	<.01	0.70
Eelgrass	<.01		0.19	0.21	0.38	0.22	0.36
Emergent grass	0.84	0.19		0.58	0.70	0.05	0.67
Hydrilla	0.18	0.21	0.58		0.94	0.02	0.52
Water lily	0.46	0.38	0.70	0.94		0.13	0.55
Pondweed	<.01	0.22	0.05	0.02	0.13		0.25
Spikerush	0.70	0.36	0.67	0.52	0.55	0.25	

Table 1-5. Proportion of total biomass comprised of adult bluegill by habitat

Habitat	Proportion of total biomass comprised of adult bluegill
Bulrush	0.79
Eelgrass	0.29
Emergent grass	0.45
Hydrilla	0.34
Water lily	0.56
Pondweed	0.38
Spikerush	0.73

Table 1-6. Analysis of Variance multiple comparison p-values for proportion of total biomass comprised of adult bluegill among habitats.

	Bulrush	Eelgrass	Emergent grass	Hydrilla	Water Lily	Pondweed	Spikerush
Bulrush		<.01	<.01	<.01	0.33	<.01	0.86
Eelgrass	<.01		<.01	0.18	0.05	0.02	0.06
Emergent grass	<.01	<.01		0.06	0.52	0.22	0.34
Hydrilla	<.01	0.18	0.06		0.14	0.37	0.13
Water lily	0.33	0.05	0.52	0.14		0.25	0.67
Pondweed	<.01	0.02	0.22	0.37	0.25		0.19
Spikerush	0.86	0.06	0.34	0.13	0.67	0.19	

Table 1-7. Proportion of total biomass comprised of adult redear sunfish by habitat

Habitat	Proportion of total biomass comprised of adult redear sunfish
Bulrush	0.52
Eelgrass	0.22
Emergent grass	0.44
Hydrilla	0.48
Water lily	0.60
Pondweed	0.36
Spikerush	0.59

Table 1-8. Analysis of Variance multiple comparison p-values for proportion of total biomass comprised of adult redear sunfish among habitats.

	Bulrush	Eelgrass	Emergent grass	Hydrilla	Water Lily	Pondweed	Spikerush
Bulrush		<.01	0.44	0.61	0.68	0.02	0.71
Eelgrass	<.01		<.01	<.01	<.01	<.01	<.01
Emergent grass	0.44	<.01		0.66	0.40	0.39	0.42
Hydrilla	0.61	<.01	0.66		0.51	0.06	0.54
Water lily	0.68	<.01	0.40	0.51		0.13	0.96
Pondweed	0.02	<.01	0.39	0.06	0.13		0.13
Spikerush	0.71	<.01	0.42	0.54	0.96	0.13	

Table 1-9. Proportion of total biomass comprised of adult black crappie by habitat

Habitat	Proportion of total biomass comprised of adult black crappie
Bulrush	1.00
Eelgrass	0.88
Emergent grass	0.91
Hydrilla	0.77
Water lily	1.00
Pondweed	0.99
Spikerush	.

Table 1-10. Analysis of Variance multiple comparison p-values for proportion of total biomass comprised of adult black crappie among habitats.

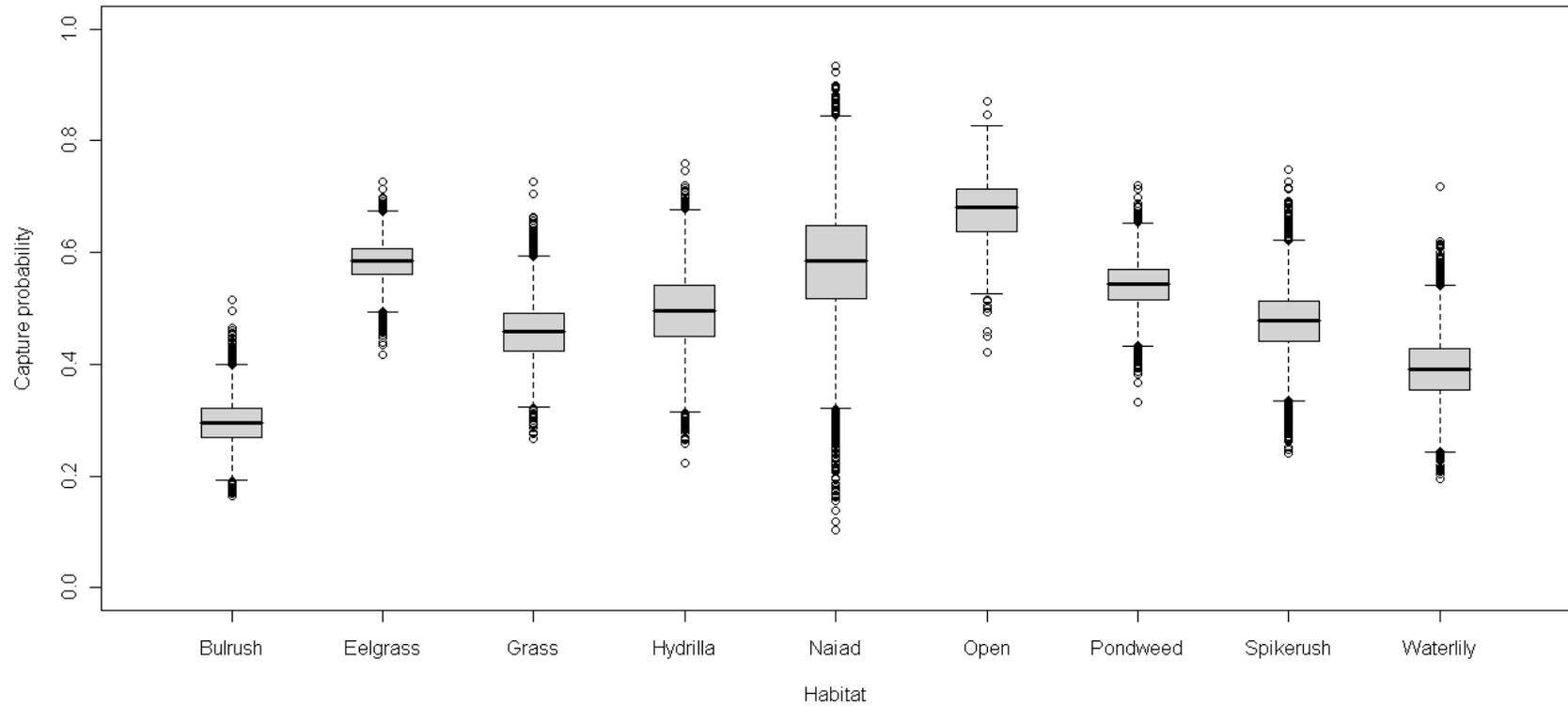|	Bulrush	Eelgrass	Emergent grass	Hydrilla	Water Lily	Pondweed	Spikerush
Bulrush		0.14	0.39	<.01	0.99	0.88	.
Eelgrass	0.14		0.80	0.05	0.61	0.08	.
Emergent grass	0.39	0.80		0.12	0.70	0.39	.
Hydrilla	<.01	0.05	0.12		0.29	<.01	.
Water lily	0.99	0.61	0.70	0.29		0.95	.
Pondweed	0.88	0.08	0.39	<.01	0.95		.
Spikerush	.	.	.	.	.	.	

. = unestimable

Figure 1-1. Capture probabilities with 95% credible intervals for 0.08 ha block nets from varying habitat types at Lake Okeechobee. Capture probabilities were estimated using a Bayesian hierarchical model and performing 10,000 Markov Chain Monte Carlo simulations (Grass = *Paspilidium spp.*).
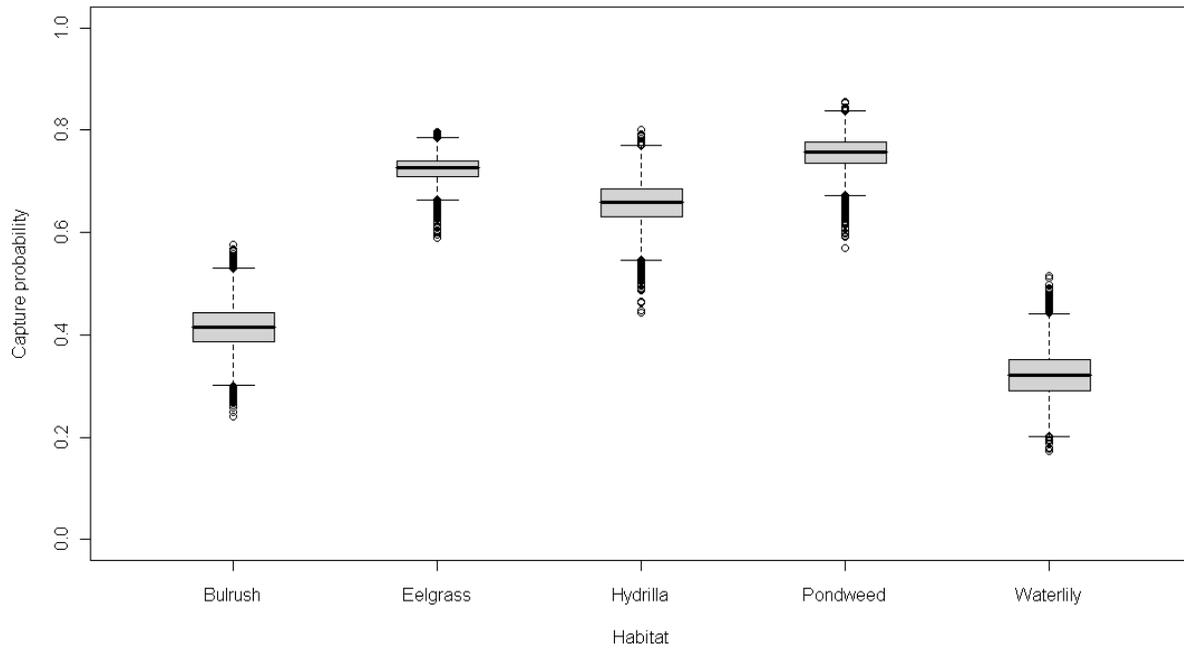
Figure 1-2. Capture probabilities with 95% credible intervals for 0.004 ha Wegener rings from varying habitat types at Lake Okeechobee. Capture probabilities were estimated using a Bayesian hierarchical model and performing 10,000 Markov Chain Monte Carlo simulations.
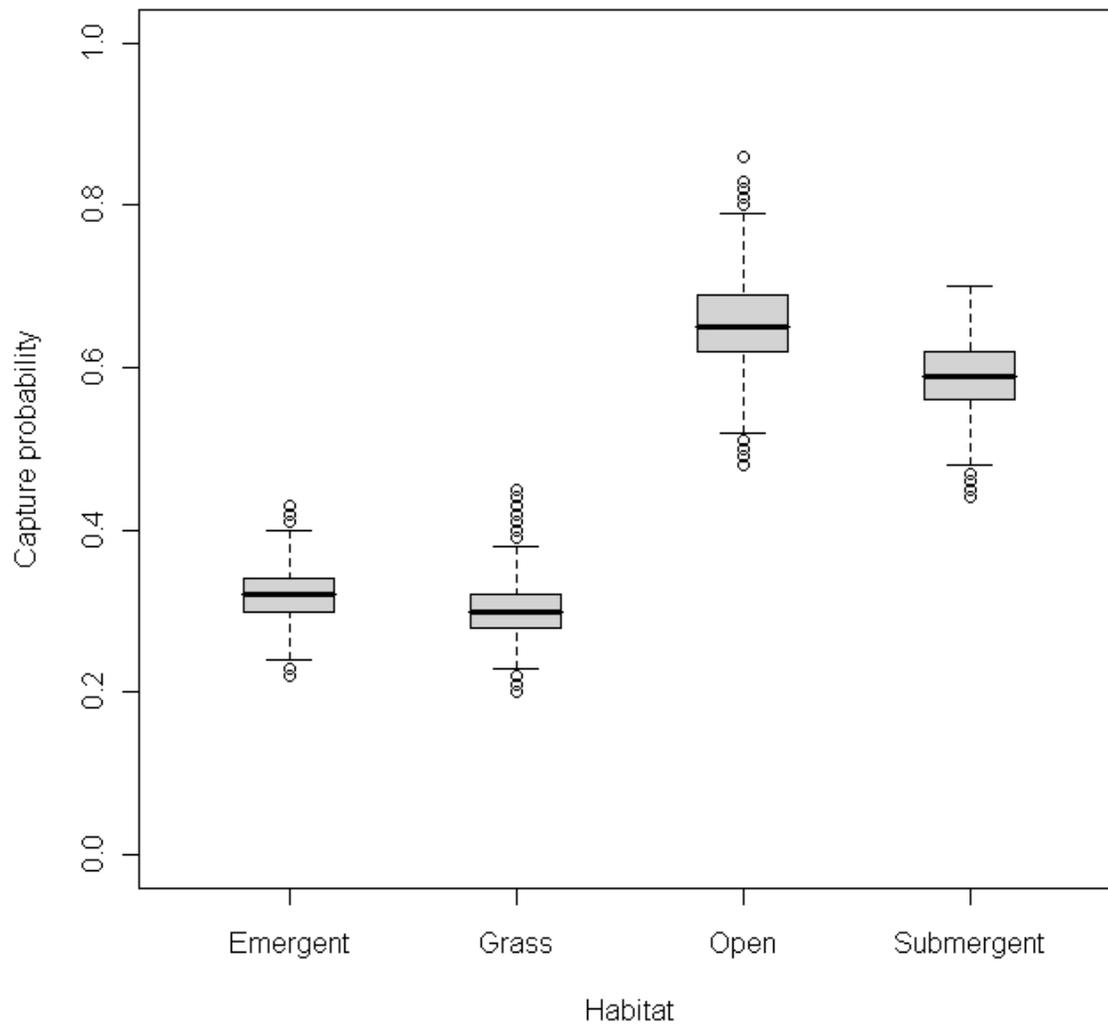
Figure 1-3. Distributions of capture probabilities with 95% confidence intervals for 0.01 ha

block nets from varying habitat types at Lakes Dora, Istokpoga, and Kissimmee. Capture

probabilities were estimated using capture-recapture methods to estimate recovery rates and re-

sampling those estimates 1,000 times to create the expected distribution for capture probability

within each habitat type. (Emergent = bulrush and spikerush, Grass = emergent grass species,

e.g., *Paspilidium spp.,* open = open water, and submergent = e.g., eelgrass and pondweed).
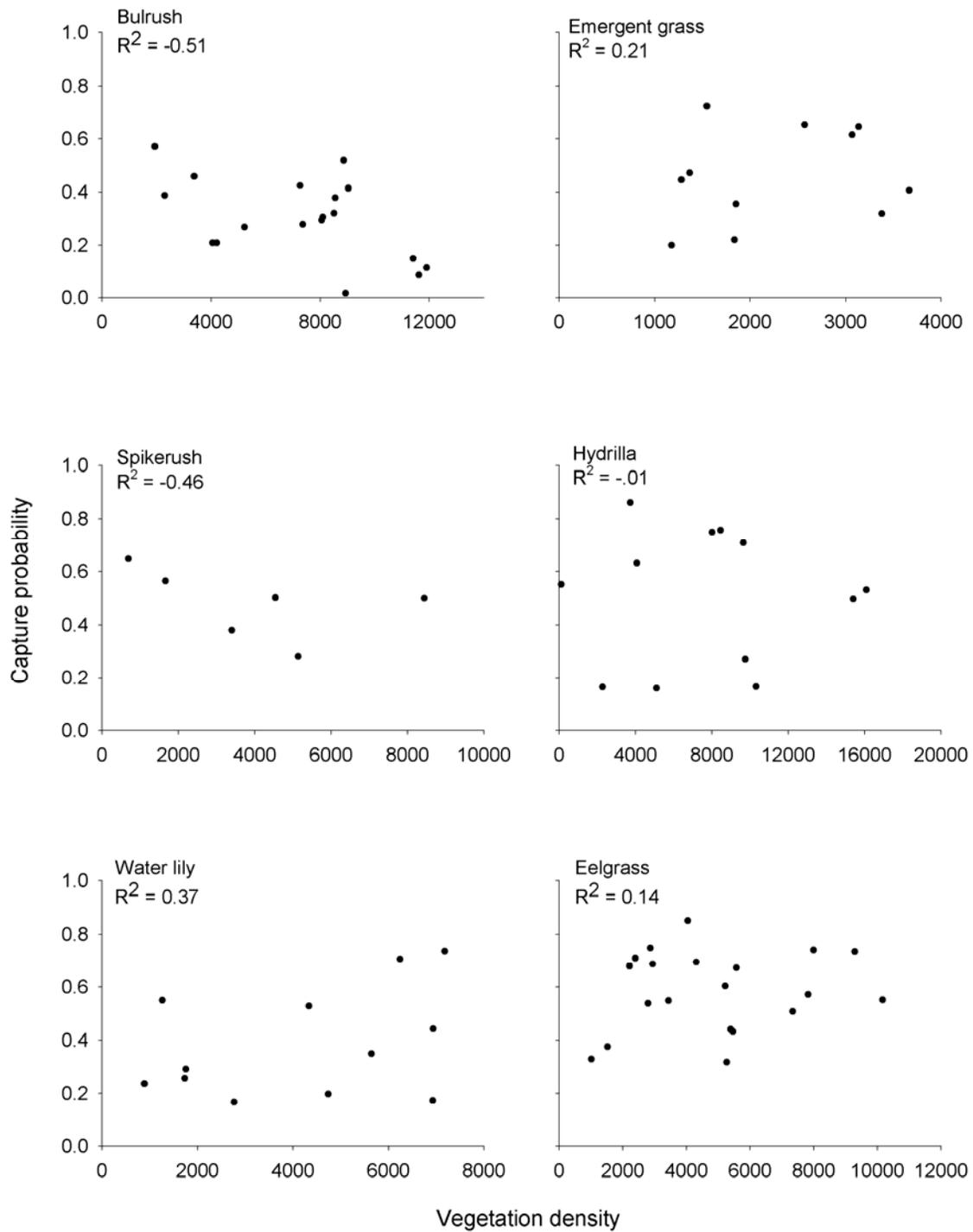
Figure 1-4. Relationships between capture probability estimates and stem densities in 0.08 ha block nets at Lake Okeechobee, Florida.

Figure 1-5. Biomass per hectare with 80% confidence intervals for functional groups collected

using 0.08 ha block nets at Lake Okeechobee, Florida. Data were corrected for capture probability in

each habitat.
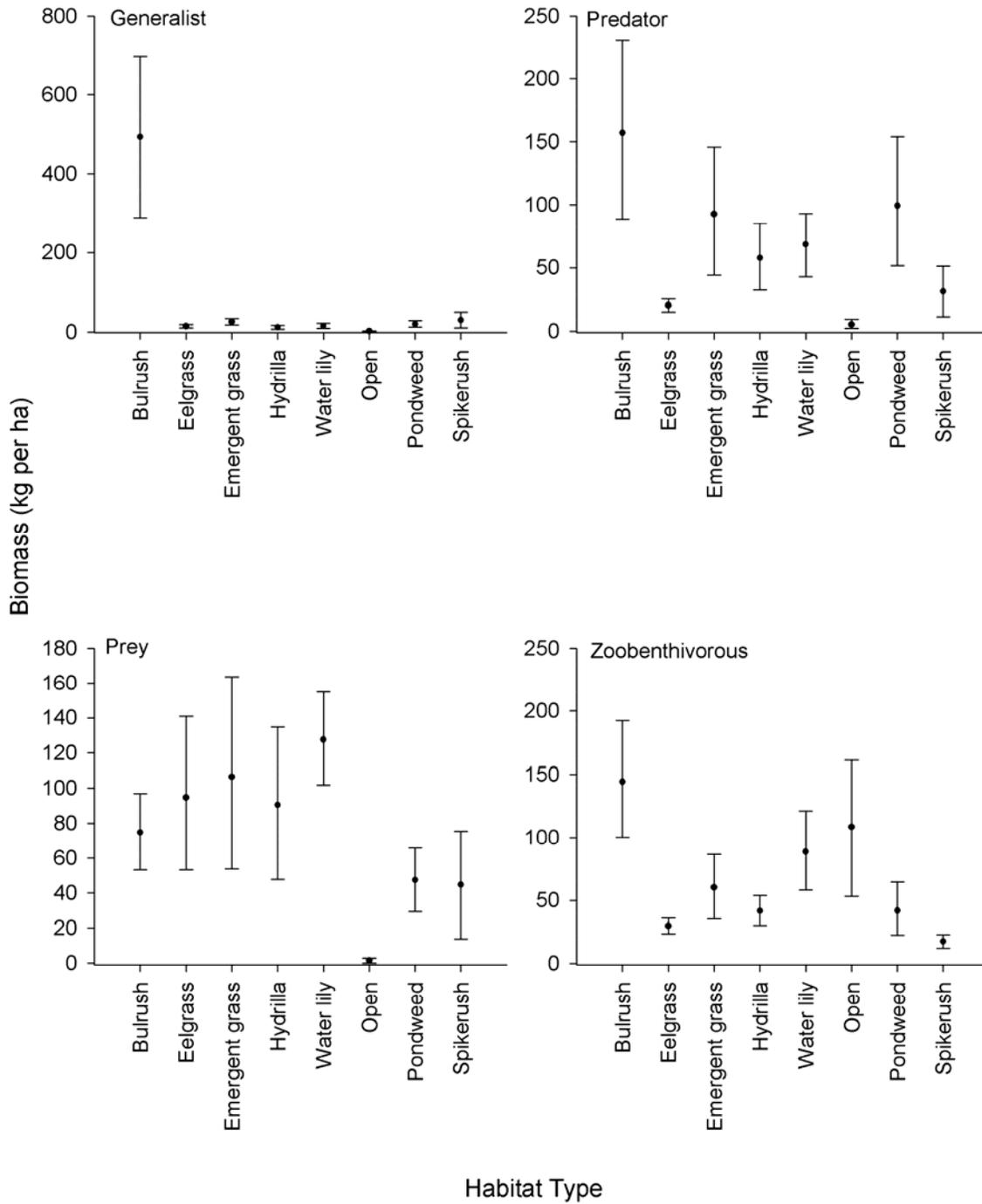
Figure 1-5 continued.
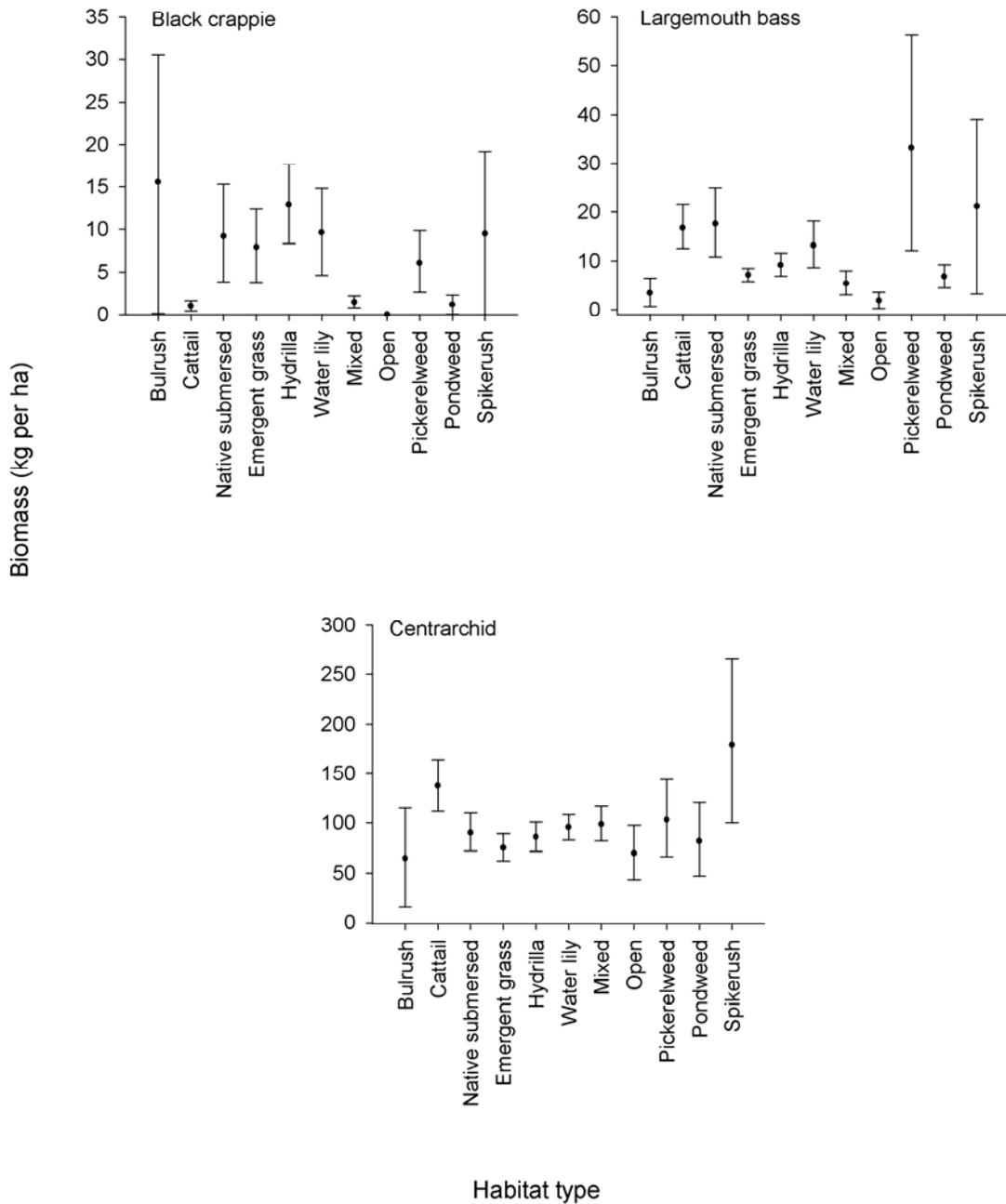
Figure 1-6. Biomass per hectare with 80% confidence intervals for functional groups collected using 0.01 ha block nets at Lakes Harris, Istokpoga, Kissimmee Monroe, Okeechobee, Seminole, and Talquin, Florida. Data were corrected for capture probability.
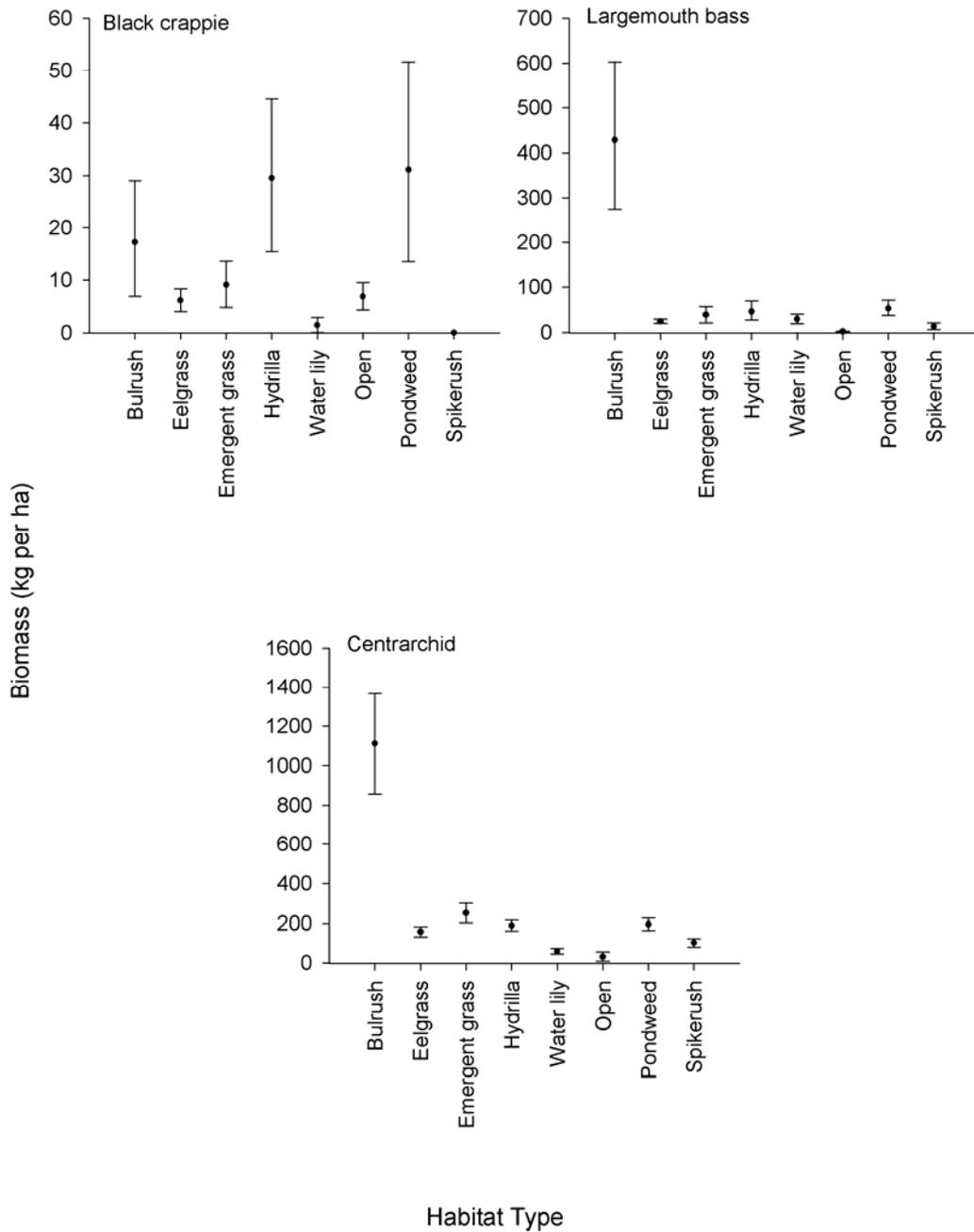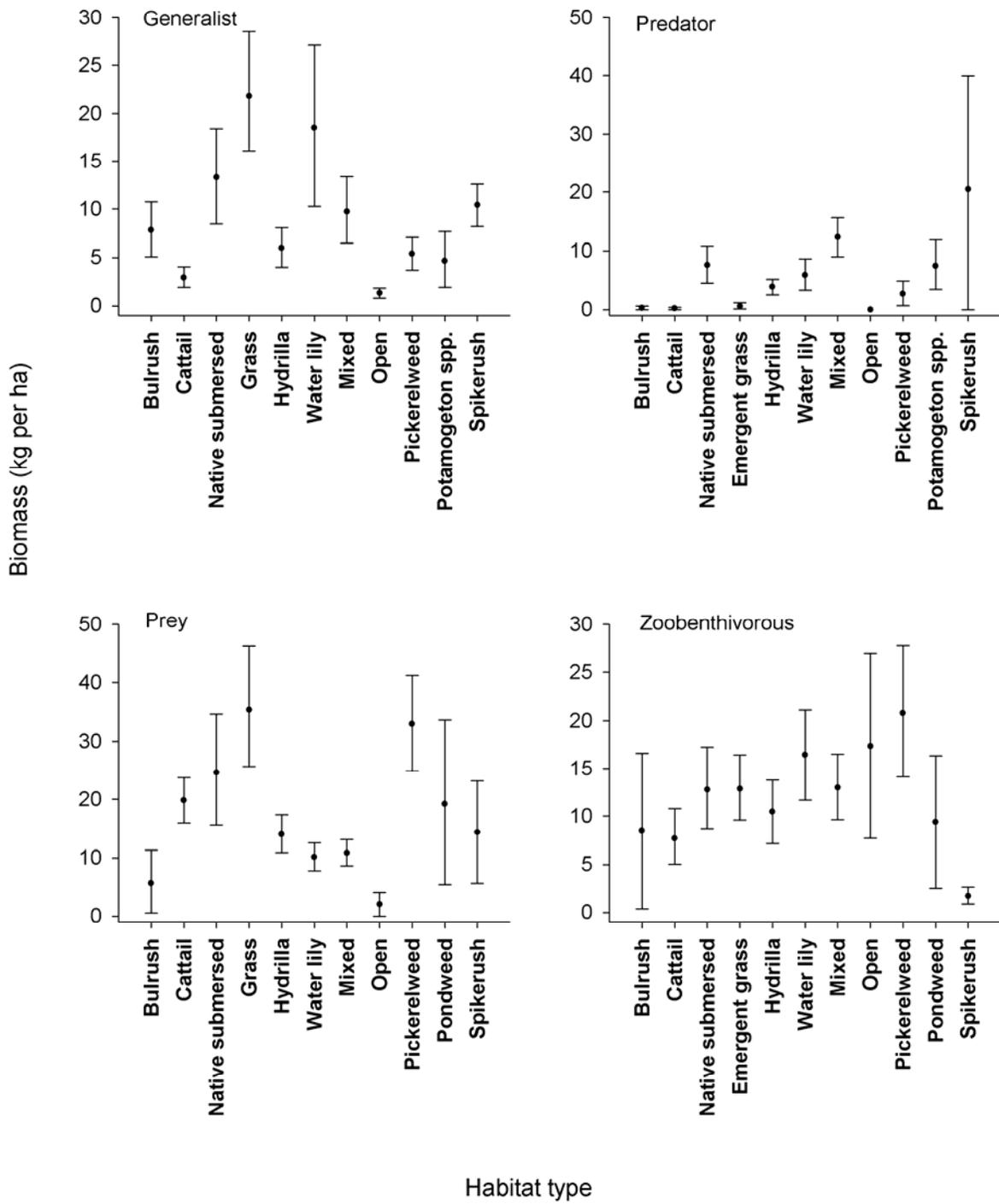
Figure 1-6 continued.
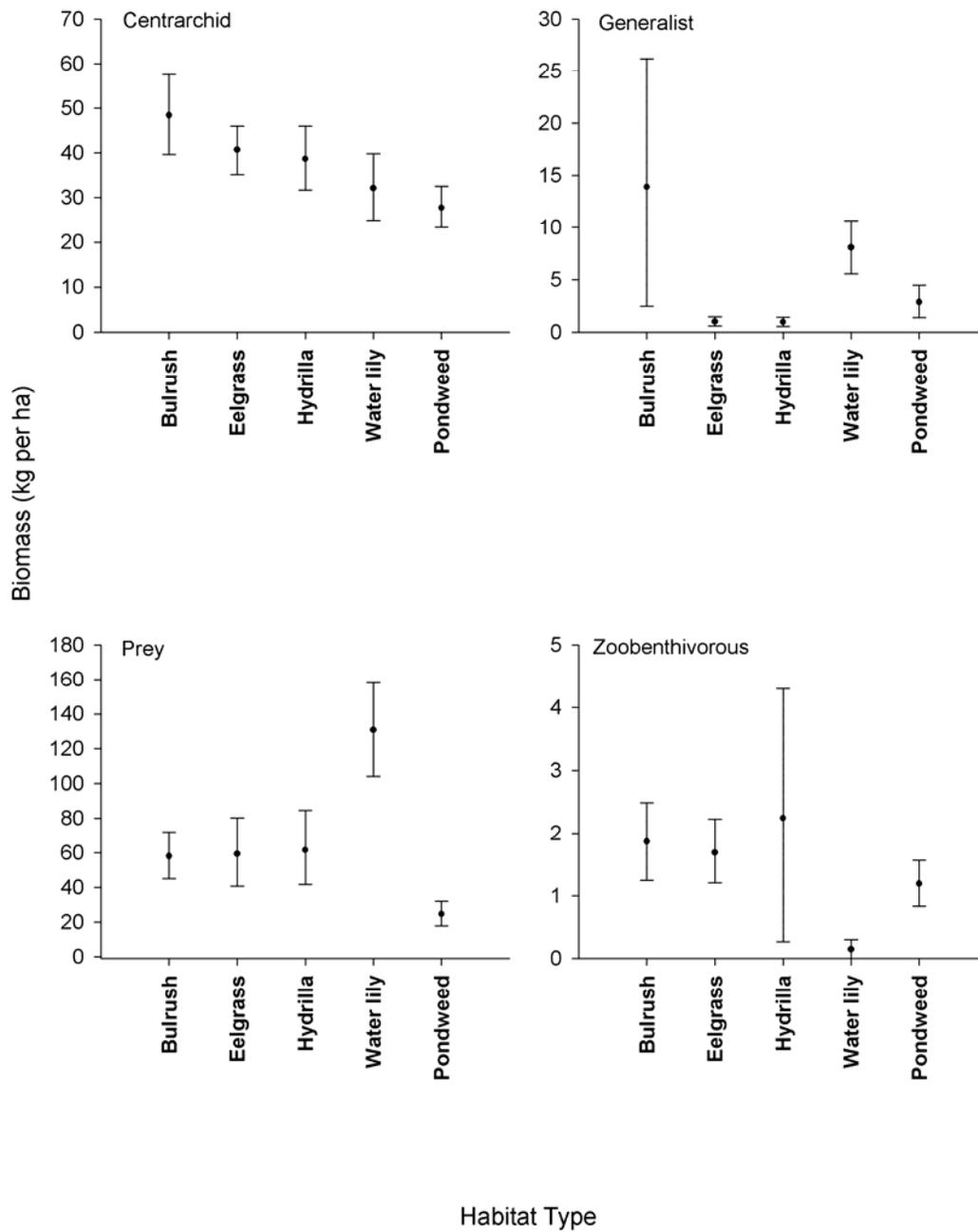
Figure 1-7. Fish biomass per hectare with 80% confidence intervals for functional groups collected using Wegener rings at Lake Okeechobee, Florida. Data were corrected for capture probability.
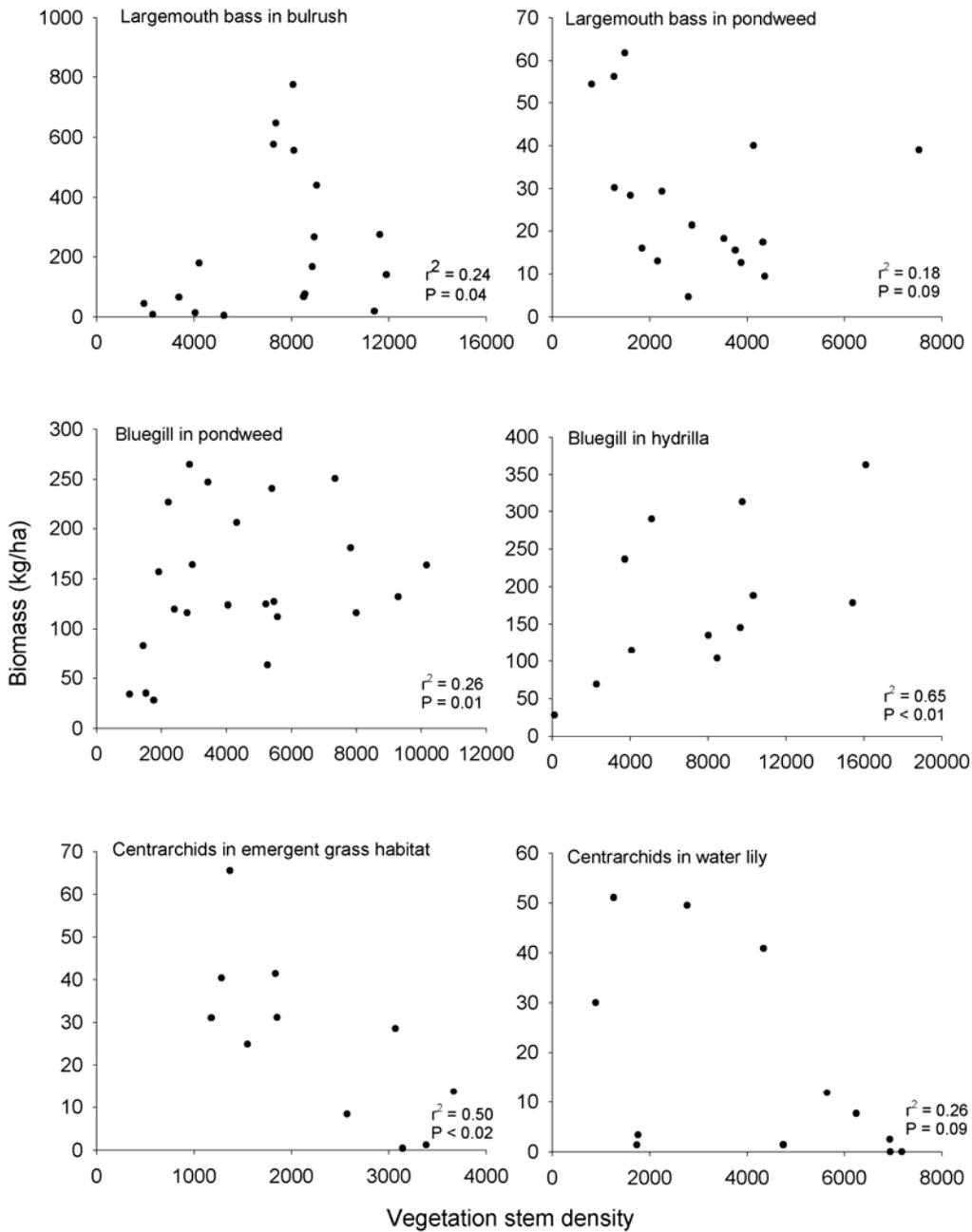
Figure 1-8. Relationships between functional group biomass and vegetation density for 0.08 ha block nets (only relationships that were significant (P < 0.10) are shown, data were log$_e$-transformed for regression analysis).
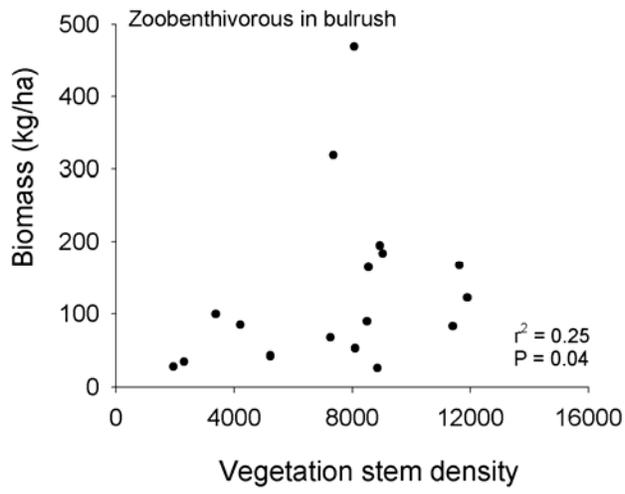
Figure 1-8 *continued*.
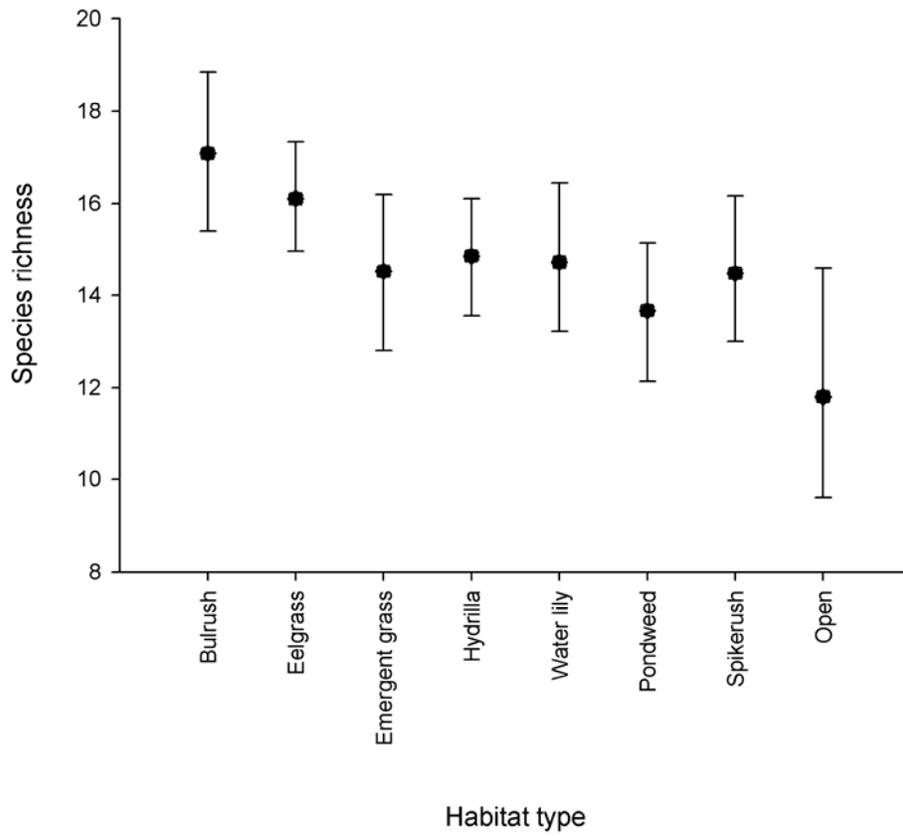
Figure 1-9. Mean species richness with 95% confidence intervals for habitats sampled at Lake Okeechobee using 0.08 ha block nets.
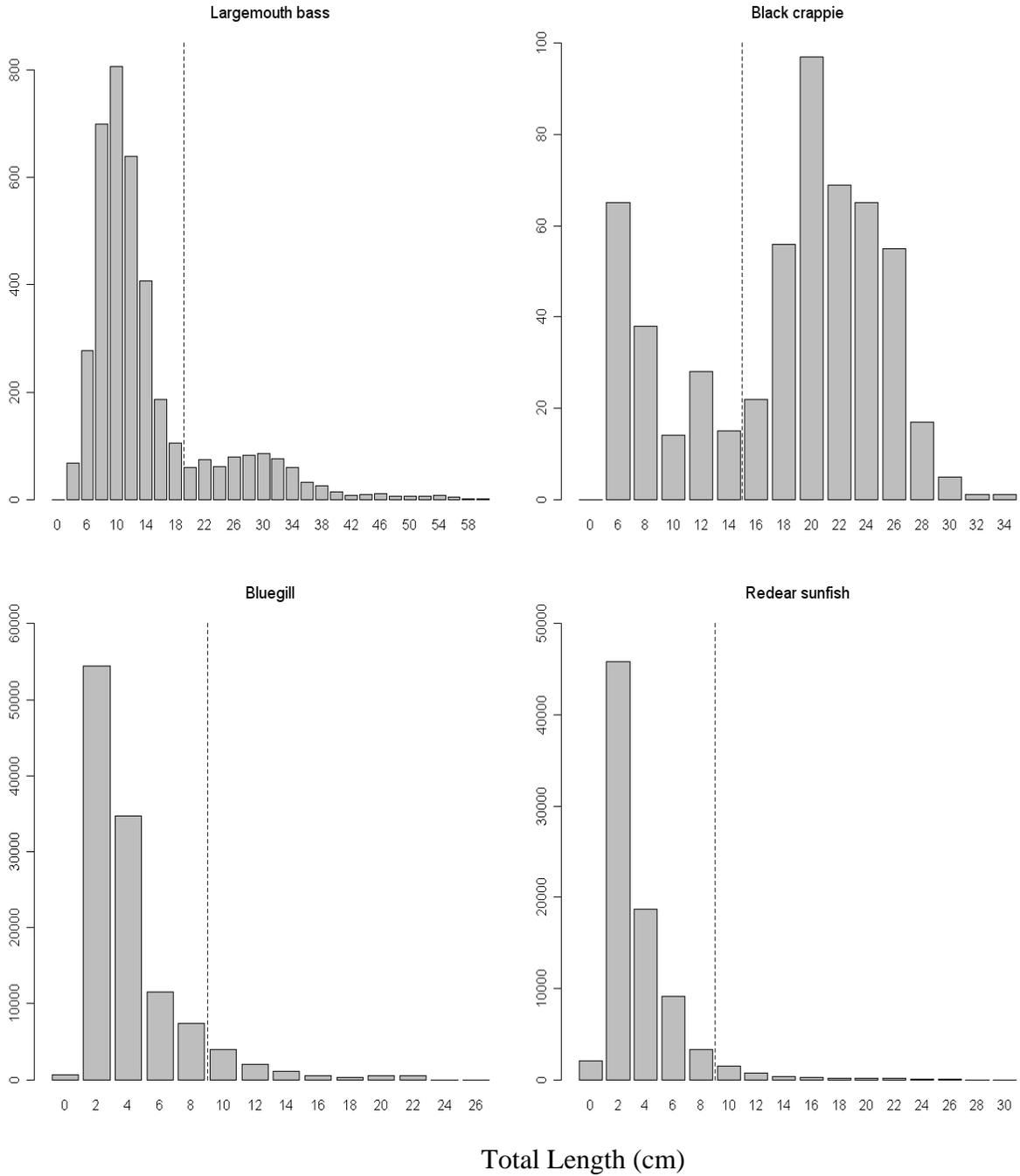
Figure 1-10. Length frequency for sport fish at Lake Okeechobee, Florida collected using 0.08 ha block nets and 0.0004 ha Wegener rings. The vertical dashed lines delineate adult and subadult size classes.

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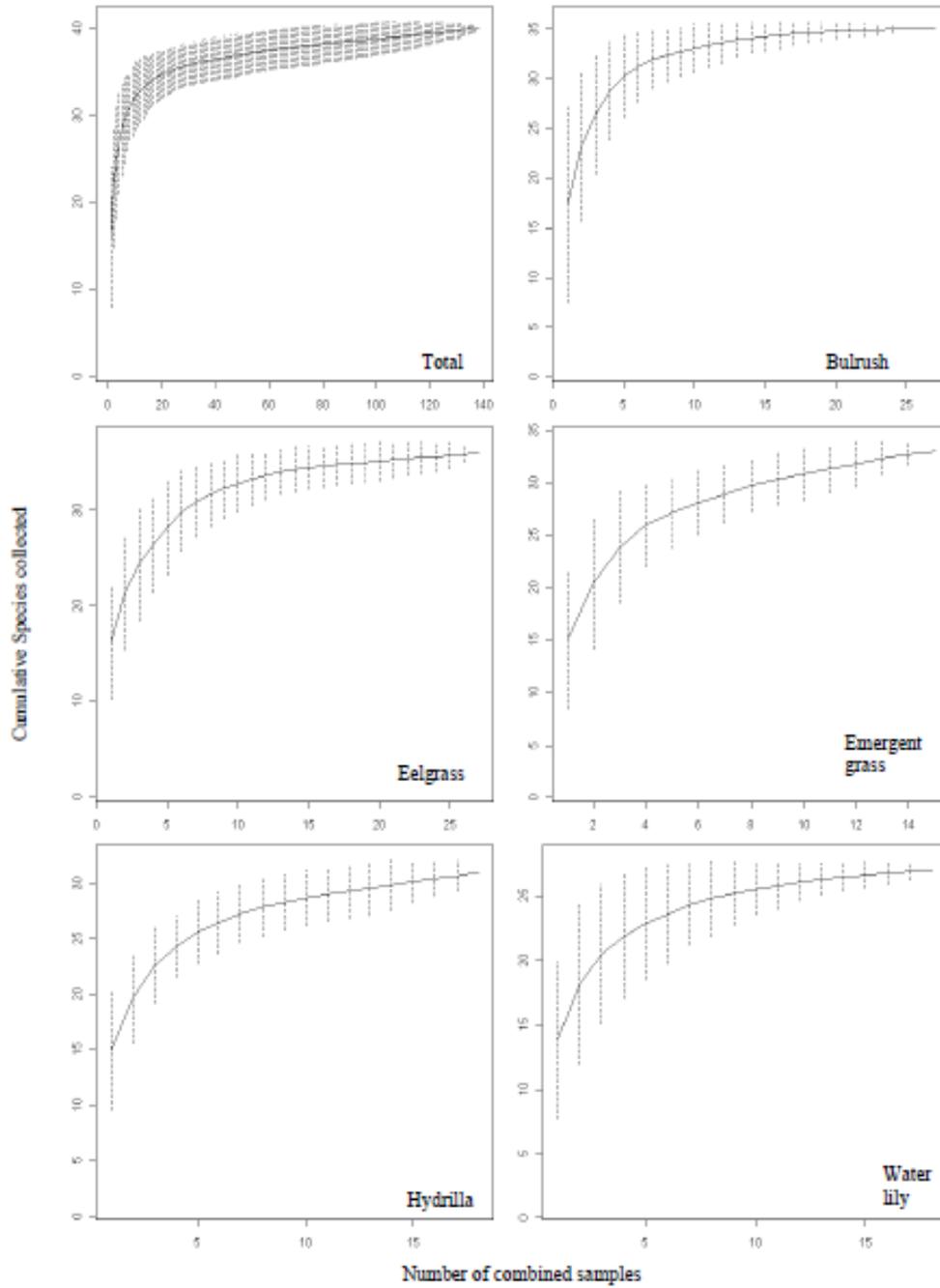
Figure 1-11. Total species accumulation with 95% confidence intervals as a function of 0.08 ha block net sampling effort.
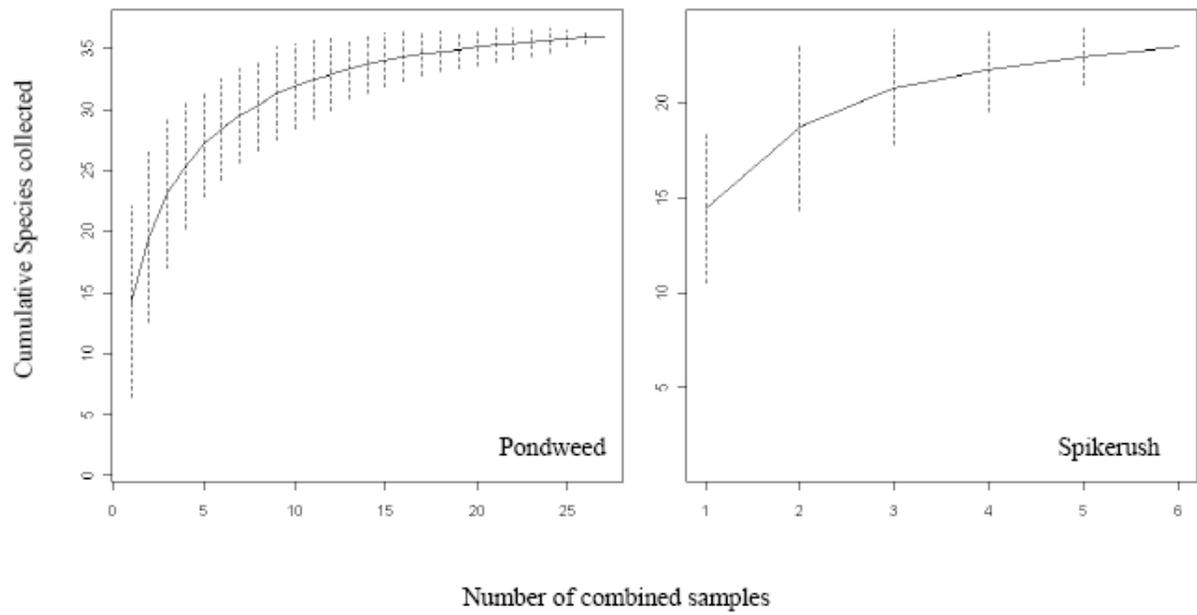
Figure 1-11 continued.
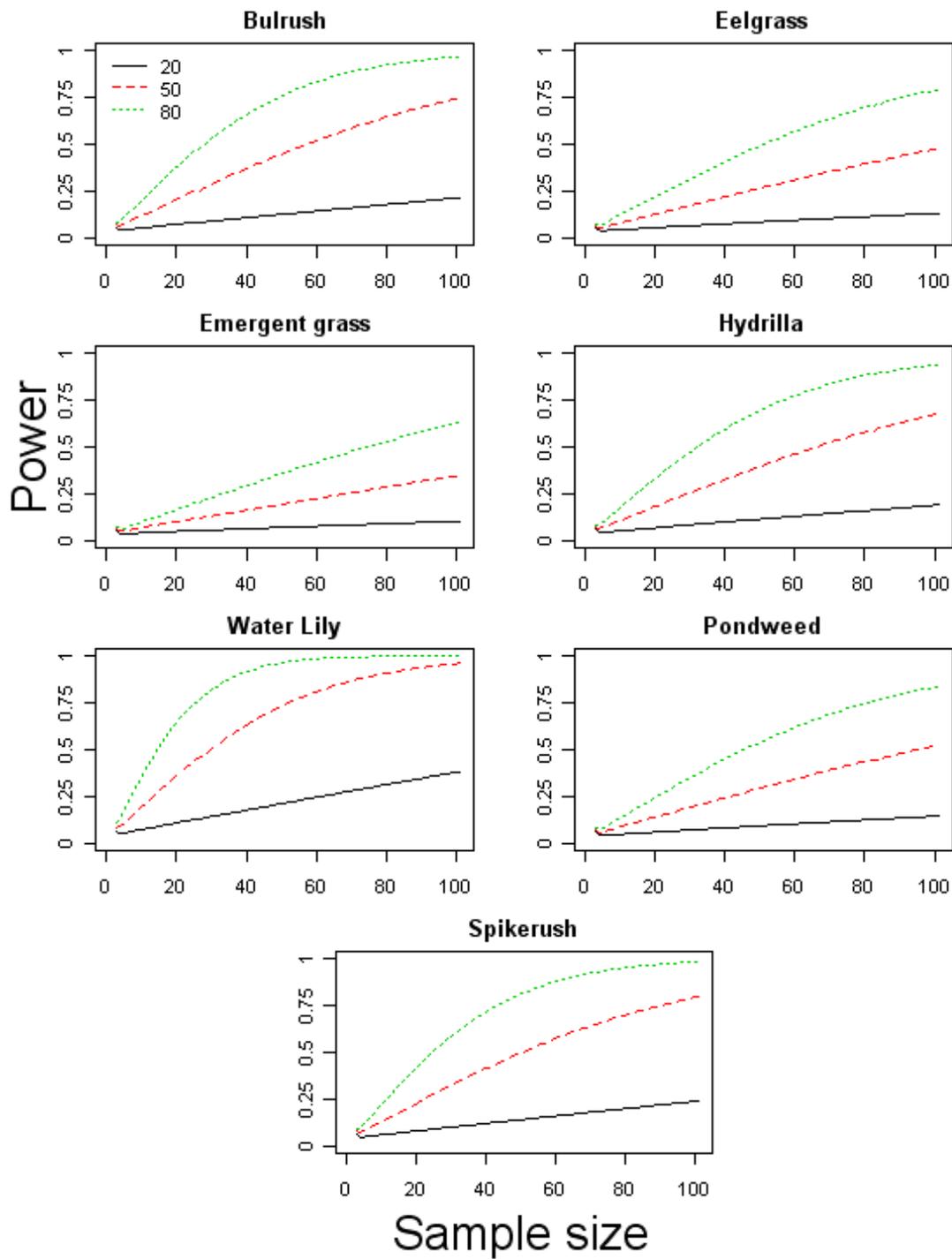
Figure 1-12. Power to detect changes in total abundance with increased sampling effort using 0.08 ha block nets.
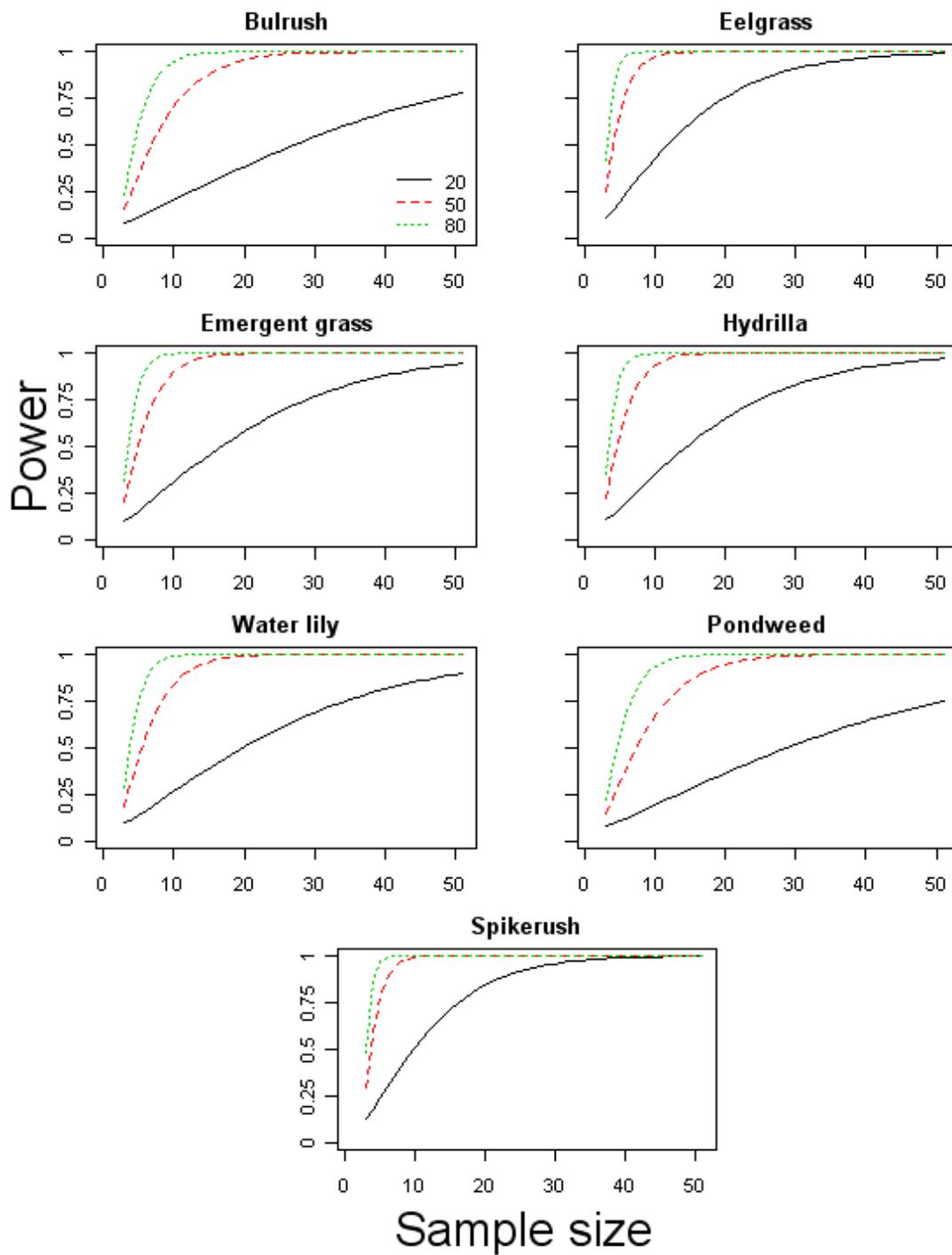
Figure 1-13. Power to detect changes in species richness with increased sampling effort using 0.08 ha block nets.
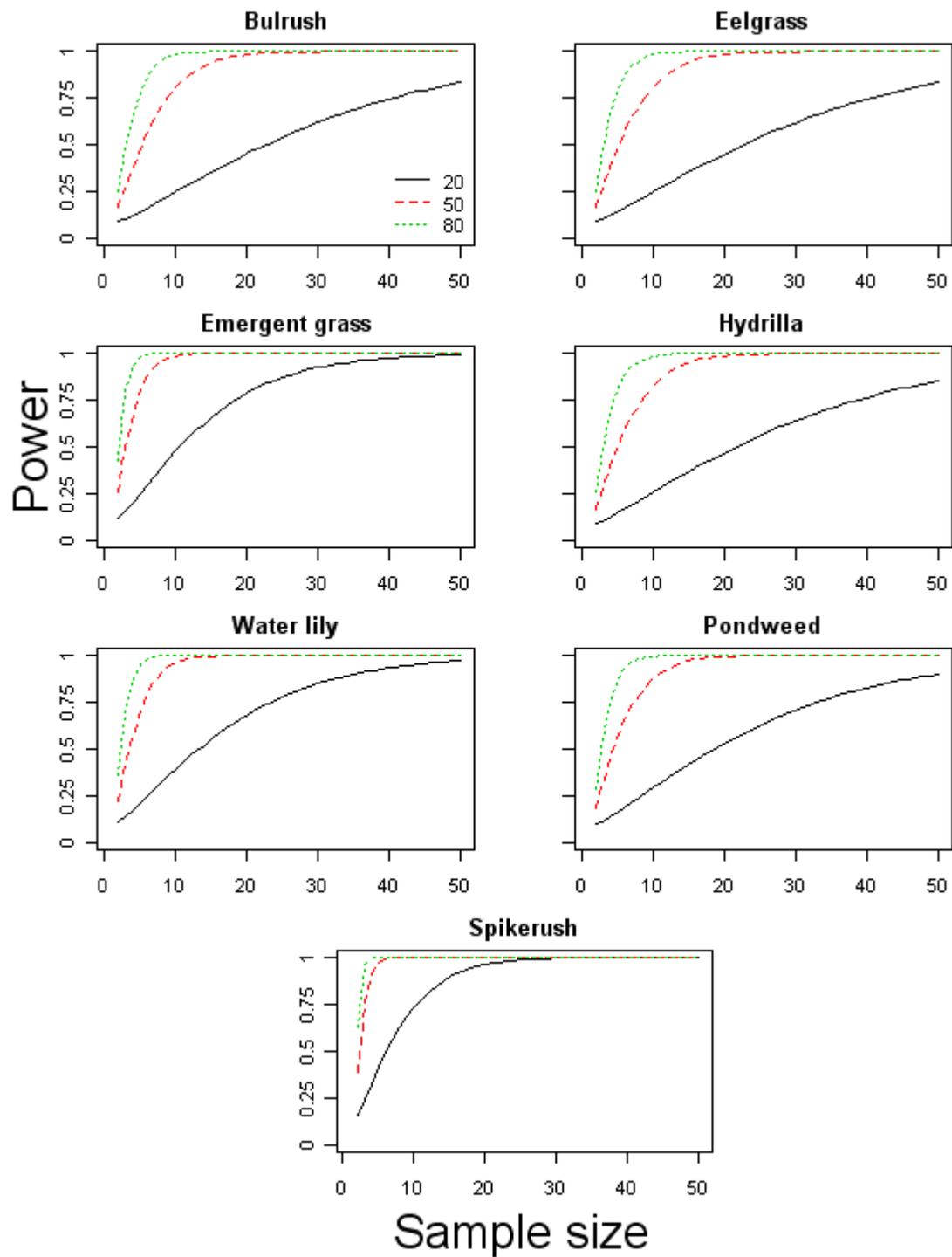
Figure 1-14. Power to detect changes in Shannon-Weiner species diversity with increased sampling effort using 0.08 ha block nets.

Chapter 2: Ecosystem Modeling to Evaluate Habitat Restorations

In this chapter we constructed an ecosystem model representing a large, eutrophic Florida lake and used the model to investigate how changes in aquatic habitats were predicted to influence fish community composition and abundance (i.e., Objectives 2 and 3). We used the ecosystem model to explore fish community and fisheries responses to habitat restoration (i.e., tussock removal) projects, which is a major habitat management challenge in systems with altered hydrology and stabilized water levels.

Overview of Ecopath with Ecosim/Ecospace

We constructed our ecosystem model using Ecopath with Ecosim (EwE; available for free download at: www.ecopath.org), which provides a framework for modeling trophic flows in an ecosystem and a dynamic simulation tool to predict how manipulations or perturbations to the system may affect its components. Ecopath incorporates user inputs to establish a mass-balanced snapshot of the ecosystem that is connected by trophic linkages among functional groups. Functional groups range from detritus/primary producers to top consumers and can be defined as groups of species, single species, or size/age groupings that are similar in their foraging ecology. The number of functional groups in the model depends on the desired complexity, data availability, and questions being investigated. In general, the Ecopath model balances inputs and outputs for all living groups though a production term and a consumption term. Data for model inputs include: biomass per area, mortality, diet composition, catches (for exploited groups), immigration/emigration, and consumption rates for each group. Ecopath specifically requires: biomass (B; kg/ha), production to biomass (P/B; yr^{-1}), consumption to biomass (Q/B; yr^{-1}) and/or ecotrophic efficiency (EE). The production to biomass ratio is equivalent to instantaneous total

mortality (Z) for fish groups and turnover rates for invertebrates and producers. The EE is the

proportion of the total mortality rate (Z) explained in the model by predation and fishing

harvests, and thus, must not exceed production inputs. Functional groups in the model are linked

through predator-prey interactions that are determined by diet composition and consumption

rates for each group. Ecopath outputs provide the framework for exploring potential management

actions and policy decision effects on the ecosystem with Ecosim and Ecospace.

Ecosim explores how simulated perturbations will influence functional group biomass

changes relative to Ecopath's baseline (balanced) conditions. Ecosim is flexible in how system

perturbations can be modeled, but most common applications involve varying a functional

group's mortality (e.g., increased fishing) or system productivity relative to baseline Ecopath

conditions. Ecosim primarily predicts changes in biomasses through time as a result of

simulated modifications (e.g., fishing policy changes, nutrient inputs, predator-prey interactions)

that affect ecosystem relationships. Ecosim works in a "foraging arena" framework where prey

vulnerabilities to predators largely structure trophic dynamics, and vulnerability can be modified

through changes in biomass, recruitment, exploitation, etc. (Walters and Martell 2004).

Vulnerability values for each consumer group on each prey type are required inputs of Ecosim

and represent the maximum predation mortality a predator can exert on a prey functional group

relative to baseline (i.e., Ecopath) predation. Low vulnerabilities (e.g., close to one) for a prey

functional group represent slow flows from the invulnerable to the vulnerable state and make

prey availability to predators largely independent of predator biomasses. High vulnerabilities

(e.g., 100) represent fast flows from the invulnerable to vulnerable state and result in large

increases in predation mortality for a prey functional group following increased predator biomass

(Christensen et al. 2005). High vulnerability values result in unstable and highly cyclic predator-

prey dynamics (e.g., Lotka-Volterra models), which are not typical of dynamics seen in nature. Vulnerability parameters are generally set at moderate levels (e.g., 2) to allow for relatively stable community dynamics typically seen in natural systems (Walters and Martell 2004).

Key aspects of Ecosim include its ability to incorporate linkages between juvenile groups and adults, mediation effects, and forcing functions. Linking juveniles groups to adults allows for ontogenetic stages such that system modifications that affect any life-stage are carried through to the population level. Incorporating mediation effects allow for a specified group to indirectly affect the predator-prey relationships between two other groups by increasing or decreasing vulnerabilities. Forcing functions allow environmental drivers (e.g., nutrient loading) to influence trophic interactions. Thus, Ecosim provides a flexible simulation tool for evaluating changes to Ecopath baseline conditions on a lake-wide scale through time.

Ecospace is a spatially explicit component of Ecopath with Ecosim that allows for habitat-specific system structure, thus allowing users to define heterogenous spatial use and behavior of functional groups. Ecospace allows users to identify up to eight ecosystem habitat types and assign each of these habitats as preferred or non-preferred for each functional group in the model. Ecospace habitats are most often delineated by depth strata or some other known gradient that influences functional group distributions. Species group dynamics follow Ecopath baseline dynamics in preferred habitats, whereas their performance is inhibited in poor habitats due to reduced feeding rates and increased predation risk in non-preferred habitats. Thus, Ecospace provides a simulation tool for evaluating changes in Ecopath baseline conditions in a spatial and habitat-specific context.

Methods

Ecopath model

Inputs for the model were obtained from the analysis in Chapter 1 and other literature sources. Functional groups in the model were linked through predator-prey interactions that were determined by diet composition and consumption rates for each group (fish groups shown in Table 2-1). Basic inputs for our Ecopath model and their sources are presented in Table 2-2. Diet composition inputs in Ecopath were entered as proportion by weight. We attempted to obtain diet composition information from studies at eutrophic Florida lakes with vegetated habitats, however many diet studies only reported percent composition by number. Diet composition inputs and their sources are presented in Table 2-3.

Fisheries were defined in the model for adult largemouth bass, adult black crappie, and adult bluegill-redear functional groups. Fishing mortality rates were entered as landings (kg/ha/yr) to result in published exploitation rates (U). Exploitation rates for largemouth bass, black crappie, and redear sunfish/bluegill were 0.18 (Allen et al. 2008), 0.40 (Allen and Miranda 1995; Allen and Pine 2000), and 0.14 (Crawford and Allen 2006), respectively. We incorporated age structure into the model for popular sport fish (i.e., largemouth bass, black crappie, and redear sunfish/bluegill groups) to incorporate ontogenetic diet shifts and habitat use.

We modeled the vegetation in a hypothetical Florida lake, but vegetation characteristics were set to mimic existing water bodies. Biomasses of specific vegetation types were derived by apportioning our estimate of total vegetation biomass per area (from Chapter 1) by percent composition of floating, emergent, native submersed, hydrilla habitat types reported for Lake Okeechobee (Bull et al. 1991). The ratio of vegetated habitat to open water (15% versus 85%) was estimated using ArcGIS maps for Lakes Kissimmee and Istokpoga provided by the Florida

Fish and Wildlife Conservation Commission (FWC unpublished data provided by Boyd Thompson, FWC, Eustis, Florida). We used the biomass accumulation tool in Ecopath for the tussock functional group to allow biomass increases through time. The tussock functional group represented dense emergent plants (e.g., pickerelweed) that had poor dissolved oxygen and low habitat suitability for centrarchids. We also set up a fishery with removals that equaled the user-input biomass accumulation rate for tussocks, which allowed for tussock biomass increases in the absence of control measures (suggested by Villy Christensen). Thus, we attempted to replicate the expansion of tussock habitat that commonly results from stabilized water levels at eutrophic Florida lakes (Moyer et al. 1995).

Ecopath mass balance is achieved when inputs (e.g., production, growth) equal outputs (e.g., predation mortality, fishing mortality) across all groups, and model balance does not occur if any group's EE exceeds Z (i.e., combined mortality explained in the model exceeds total instantaneous mortality) for that group. If a model is not balanced (i.e., ecotrophic efficiency exceeds one for any group), Ecopath provides several diagnostic measures (e.g., predation mortality from each of the other functional groups) that can inform the user of potential input errors. We balanced our model using an iterative method (see Christensen et al. 2005) rather than the auto-mass balance tool (Kavanaugh et al. 2004) in Ecopath. Input parameters were adjusted to reach model balance based on knowledge of the data source and realistic ranges in parameter values from published sources. Fish group biomasses were not adjusted to reach model balance because those data were estimated from historical FWC block net data (i.e., Objective 1). Diet composition and invertebrate biomasses were most commonly adjusted because those data were often derived from an online database (i.e., www.fishbase.org) and other studies. We did not adjust age-0 largemouth bass diet composition that was obtained from

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Rogers and Allen (2005). After achieving balance, we used the Ecoranger sensitivity routine to perturb our model inputs and evaluate the dominant causes of model failures (i.e., imbalance).

Ecosim simulations

We used Ecosim to perturb the balanced Ecopath model and explore how lake restoration activities were predicted to influence fish communities and fisheries. Specifically, we simulated the effects of tussock accumulation on fish communities and fisheries and results of differing tussock controls. We evaluated three scenarios in Ecosim: 1) a baseline "no control" option where tussocks were allowed to increase to > 2x the initial biomass, 2) a "10-year control" option that reduced tussock biomass to near baseline levels every 10 years, and 3) "combined control", which reduced tussock biomass every 10 years and also used control measures in the interim to maintain lower biomass relative to scenario 1. Fish community and fishery metrics were predicted biomass per area and fishery catch per area for each scenario at a whole-lake scale.

Vulnerability inputs for functional groups were either estimated by Ecosim, directly input based on historical data, or we used the default (v = 2.0) value (Table 2-4). We attempted to estimate vulnerabilities, when possible, by incorporating historical data. For some groups (e.g., largemouth bass) we were able to use historical time series of relative abundance indices (e.g., electrofishing data) and use the variability to estimate the vulnerability using a model fitting routine in Ecosim that was constrained by predator and prey linkages. Historical data also allowed us to inform vulnerability inputs based on minimum and maximum abundances for some groups (e.g., centrarchid group), thus providing information on the magnitude of expected biomass variability. For many of the lower trophic level groups we used the default value of 2.0

because time series data were not available. We also set feeding time adjustment rates to zero for groups (e.g., predators, adult sport fish) that were not expected to exhibit highly risk-sensitive foraging behaviors (suggested by Carl Walters).

We used the mediation tool in Ecosim to represent reported patterns between fish community use and tussock habitats. The pattern was set such that increased tussock biomass was expected to: 1) create refugia for prey species used by juvenile sport fish and centrarchid groups, and 2) reduce abundance of juvenile sport fish and centrarchid groups (simulated by increased mortality). Thus, our mediation effects caused increased tussock biomass to result in poor quality habitats for juvenile sport fish and centrarchid groups and suitable habitats for species commonly found in tussock habitats (e.g., our prey fish functional group, Table 2-1). Fish species affected by mediating factors (i.e., tussock biomass) were derived from sampling dense emergent plants (>70% coverage) at Lake Kissimmee that indicated nearly all biomass in these habitats were represented by species within our prey fish functional group (Bunch et al. 2008). We simulated tussock biomass affects on habitat quality by altering predator-prey interactions because the model could not explicitly incorporate water quality parameters (i.e., low dissolved oxygen) that have been identified by other researchers (e.g., Tugend and Allen 2004; Bunch et al. 2008) as limiting factors for fish survival in tussock habitats. We also set up a "tussock fishery" that reduced tussock biomass, and thus, provided a tool to simulate tussock reduction efforts such as drawdown and muck removal projects.

Ecospace simulations

We used Ecospace to evaluate how spatial coverage of tussocks within the littoral zone would influence fish group distributions and biomasses. We mapped four habitat types in

Ecospace: 1) tussock, 2) littoral, 3) nearshore, and 4) offshore, where nearshore and offshore

habitats both represented open water. The open water habitat was divided into nearshore and

offshore components to limit the spatial habitat availability of functional groups that used open

water habitats near littoral edges, but were not reported to occupy distant offshore open water

(Bull et al. 1995). We used biomass-habitat relationships identified in Chapter 1 and other

published literature to assign preferred habitats for each functional group (Table 2-5). Preferred

habitats had: increased feeding rates (2-10x), decreased predation mortality rates (0.125%-0.5%),

and decreased emigration rates (0.2%) relative to non-preferred habitats. We simulated a

restoration project that reduced lake-wide tussock coverage from 30% to 15% to evaluate

restoration effects on functional groups and fisheries.

Results

Ecosim simulations

Under baseline (i.e., "no control") conditions, tussock biomass increased over 100% and

reached an asymptote within five years. Increased tussock biomass resulted in large increases in

predator biomass (+ 31%, i.e., bowfin, gars) and grass shrimp (300%) and slight increases in

generalist fish (6%) and phytoplankton (8%; Table 2-6). Large biomass decreases were

predicted for largemouth bass and bluegill-redear functional groups with smaller magnitude

decreases for black crappie. The increase in predators and grass shrimp resulted from decreased

predation mortality. For example, grass shrimp predation mortality was reduced from > 7 yr^{-1} to

4 yr^{-1}, thus allowing for large biomass increases. Major reductions in predation mortality

resulted from decreased recruitment of largemouth bass and other sport fish as a function of our

diet composition inputs, and was further exacerbated by the mediation function relationships.

Ten-year controls that induced high tussock mortality provided short-lived (i.e., about 3 year) improvements in abundances of functional groups that were negatively affected by tussock biomass (Figure 2-1). Ten-year controls were predicted to reduce tussock biomass to baseline levels and increase production of juvenile sport fish and other species that are suggested to be intolerant of tussock habitats (Table 2-6). However, 10-year controls were not predicted to result in long-term restoration effects. In contrast, some groups (e.g., predators, prey fish) were predicted to have persistently large biomass increases under high tussock conditions. Thus, large-scale 10-year removals were predicted to provide short-term system rehabilitation, but periodic removals alone would not permanently restore fisheries or abundances of tussock-sensitive species and biomasses, which were predicted to quickly return to the same levels as the baseline no control simulations (Figure 2-1).

Combined controls provided the largest long-term biomass increases for most sport fish functional groups (i.e., except black crappie) relative to taking no action between 10-year treatment periods or no tussock treatment at all (Table 2-6; Figure 2-2). Combined controls resulted in rapid sport fish biomass increases that were maintained at the highest levels of our scenarios (Figure 2-2). Combined controls were predicted to result in a 41% increase in age-0 largemouth bass biomass relative to no control and 23% increase relative to 10-yr controls (Table 2-6). Combined controls also provided positive benefits for largemouth bass and bluegill-redear fisheries relative to other simulation scenarios (Table 2-6). Thus, combined use of infrequent tussock removal and herbicide maintenance provided the greatest potential for long-term sport fish benefits relative to our other simulated habitat management options.

Ecospace Simulations

Spatial simulations that decreased tussock surface area from 30% to 15% predicted positive benefits for sport fish functional groups and fisheries (Table 2-7; Figure 2-3). The largest biomass increases were predicted for the bluegill-redear sunfish group and the centrarchid group, which both increased by > 100% following the restoration. Interestingly, black crappie fishery catches were expected to increase following the restoration despite limiting the spatial range of adult black crappie and their fisheries to nearshore and offshore habitats (i.e., the spatial areas used by these groups were not directly affected by tussock accumulation or restoration). This increase was likely due to our allowance of juvenile black crappie to use both littoral and nearshore habitats (Conrow et al. 1990), and thus, total recruitment increased following a simulated restoration. Ecospace also estimated increased biomass for all non-tussock macrophyte groups following a restoration (Table 2-7).

Ecospace provided biomass estimates for every functional group in all sketched lake-cells following our simulated restoration. Thus, our Ecospace simulation scenario resulted in 18,816 biomass per area estimates (784 lake cells x 24 functional groups) at each time step. Here, we only report biomass per area for the age-0 largemouth bass functional group because they are commonly sampled during post-restoration evaluations (e.g., Moyer 1995, Allen and Tugend 2002). We compared biomass in littoral un-restored versus restored areas following our simulated tussock removals to determine if predicted biomass per area differed between the two littoral habitat areas. Mean biomasses across all restored versus unrestored sites were 0.33 kg/cell and 0.19kg/cell, respectively. However these biomasses did not differ significantly because 90% confidence intervals overlapped. Biomass predictions had coefficients of variation that were similar (35% and 29%) for both habitat areas. Age-0 largemouth bass biomasses within tussock habitats displayed sensitivity to edge effects because estimates remained

relatively high at the interfaces between restored areas and unrestored areas (i.e., along edges of tussock habitats). Edge interfaces always had higher age-0 largemouth bass biomasses than interior areas of tussock habitats, but edge biomasses increased as the extent of nearby quality habitat increased. To control for edge effects on biomass comparisons, we re-sampled predicted biomasses (with replacement) from interior areas of restored and unrestored areas 1000 times to derive the expected mean and 90% confidence intervals for each area. Ecospace predicted significantly higher age-0 largemouth bass biomasses at restored sites relative to unrestored tussock sites. Mean biomass at restored sites was 0.41 kg/ha and 0.14 kg/ha at remaining tussock sites and 90% confidence intervals did not overlap. Thus, comparisons from within restored versus unrestored zones overestimated the true lake-wide effects of tussocks if edge habitats were ignored. In summary, Ecospace indicated that large restoration projects: 1) would benefit most sport fish groups and fisheries, 2) should consider the ability of edge effects to offset negative effects of large tussock areas, and 3) sampling designs (i.e., sampling locations and sampling intensity) of restoration assessments could largely influence the ability to detect restoration effects.

Sensitivity Analyses

We used the Ecoranger sensitivity routine to evaluate our model's reliability. Ecoranger varies model inputs (i.e., B, P/B, P/Q, and diet composition) by 20% and reports the percentage of trials that result in successfully balanced models. Ecoranger also outputs the causes for unsuccessful model balance under varied inputs. Ecoranger showed that our model's balance was most sensitive to juvenile sport fish and grass shrimp biomass inputs and incorporating variability in these inputs often resulted in ecotrophic efficiencies that exceeded one for these

groups (i.e., outputs exceeded production). High model sensitivity to juvenile fish biomasses is

not uncommon because these groups occurred at low biomasses and small increases in mortality

(e.g., diet composition of a predator) can have large effects. High sensitivity to grass shrimp

inputs were not unexpected because they commonly occur in diet composition data for many of

the functional groups. Thus, incorporating variability of grass shrimp predator inputs could

greatly increase mortality rates for this group. Model sensitivity to grass shrimp inputs

illustrated our uncertainty for this group's inputs because we borrowed biomass inputs from

other studies (e.g., Schramm et al. 1983), and their importance to diet composition of functional

groups was hard to determine because we found little diet composition data from systems where

grass shrimp likely occur. Thus, future use of this model should seek to reduce uncertainty in

diet inputs (i.e., prey composition reported by percent weight) and consumption per biomass for

higher trophic level groups (e.g., predators) that highly influence system-wide prey mortality.

Table 2-1. Species composition of fish functional groups for an Ecopath model of a large Florida eutrophic lake.

Functional group	Species composition	
Predators	bowfin	Amia calva
	chain pickerel	Esox niger
	Florida gar	Lepisosteus platyrhincus
	longnose gar	Lepisosteus osseus
Largemouth bass	largemouth bass	Micropterus salmoides
Black crappie	black crappie	Pomoxis nigromaculatus
Bluegill/Redear sunfish	bluegill	Lepomis macrochirus
	redear sunfish	Lepomis microlophus
Centrarchid	spotted sunfish	Lepomis punctatus
	dollar sunfish	Lepomis marginatus
	warmouth	Lepomis gulosus
	bluespotted sunfish	Enneacanthus gloriosus
	redbreast sunfish	Lepomis auritus
	pygmy sunfish	Elassoma sp.
Prey	golden topminnow	Fundulus chrysotus
	mosquitofish	Gambusia sp.
	seminole killifish	Fundulus seminolis
	sailfin molly	Poecilia latipinna
	least killifish	Heterandria formosa
	bluefin killifish	Lucania goodei
	lined topminnow	Fundulus lineolatus
	rainwater killifish	Lucania parva
	russetfin topminnow	Fundulus escambiae
	flagfish	Jordanella floridae
Generalists	brook silverside	Labidesthes sicculus
	atlantic needlefish	Strongylura marina
	opposum pipefish	Microphis brachyurus
	pugnose minnow	Opsopoeodus emiliae
	sheepshead minnow	Cyprinodon variegatus
	striped mullet	Mugil cephalus
	golden shiner	Notemigonus crysoleucas
	taillight shiner	Notropis maculatus
	tidewater silverside	Menidia peninsulae
	coastal shiner	Notropis petersoni
Zoobenthivorous fish	swamp darter	Etheostoma fusiforme
	lake chubsucker	Erimyzon sucetta
	tadpole madtom	Noturus gyrinus
	threadfin shad	Dorosoma petenense
	gizzard shad	Dorosoma cepedianum
	clown goby	Microgobius gulosus
	channel catfish	Ictalurus punctatus
	brown bullhead	Ameiurus nebulosus
	blue tilapia	Tilapia aurea
	white catfish	Ameiurus catus
	yellow bullhead	Ameiurus natalis
	pirate perch	Aphredoderus sayanus
	hogchoker	Trinectes maculatus
	sailfin catfish	Pterygoplichthys multiradiatus
	naked goby	Gobiosoma bosc
	black acara	Cichlasoma bimaculatum
	brown haplo	Hoplosternum littorale

Table 2-2. Inputs and data sources for a large Florida eutrophic lake Ecopath model. *Tussock represents dense macrophyte stands (100% coverage) with low habitat suitability (see Moyer et al. 1995).

Functional group	Biomass (kg/ha)	P/B (yr^{-1})	Q/B (yr^{-1})	Ecotrophic efficiency	Biomass accum. (t/km2/yr)
predators	66.00 [a]	0.25 [g]	4.00 [g]		
LMB-adult	17.50 [a]	0.63 [h]	6.00 [b]		
LMB (6 mo-3 yr)	9.25 [b]	1.00 [i]	10.87 [b]		
LMB (0-6 mo)	0.16 [b]	3.60 [j]	41.64 [b]		
black crappie adult	5.13 [a]	1.50 [k]	6.40 [b]		
black crappie (0-12 mo)	3.25 [b]	2.41 [k]	16.21 [b]		
bluegill / redear adult	56.20 [a]	0.82 [l]	6.50 [b]		
bluegill / redear (0-12 mo)	4.06 [b]	2.00 [g]	17.61 [b]		
centrarchid	46.00 [a]	1.80 [g]	16.00 [g]		
prey fish	73.00 [a]	2.42 [g]	43.40 [g]		
generalist fish	76.00 [a]	2.00 [g]	35.60 [g]		
zoobenth fish	66.00 [a]	2.12 [g]	19.70 [g]		
grass shrimp	14.70 [c]	7.92 [b]	19.00 [f]		
ephiphytic invertebrate	163.94 [c]	12.00 [f]	25.00 [f]		
benthic invertebrate	118.00 [d]	27.00 [e]	70.00 [e]		
zooplankton		20.00 [f]	70.00 [f]	0.8	
epiphytic algae	150.00 [d]	51.00 [e]			
floating leaf	35.20 [a,m]	5.00			
emergent vegetation	162.60 [a,m]	5.00			
native submersed	27.10 [a,m]	10.00			
hydrilla	46.10 [a,m]	10.00			
phytoplankton		50.00 [e]		0.8	
tussock*	25.00	5.00			15
detritus	100.00 [f]				

a	this study (objective 1)
b	estimated by Ecopath
c	Schramm et al. (1983)
d	Canfield and Hoyer (1992)
e	Ewel (1983)
f	published Ecopath models
g	www.fishbase.org
h	assumed U = 0.18 and M = 0.4
i	DeAngelis et al. (1993)
j	Rogers and Allen (2009)
k	Raborn et al. (2002)
l	Crawford and Allen (2006)
m	Bull et al. (1991)

Table 2-3. Diet composition inputs for a large eutrophic Florida lake Ecopath model. Matrix indicates diet proportion (by weight) that each group (left column) contributes to each consumer group (numbers across top)

Group number	Functional group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	predators		0.03														
2	LMB-adult																
3	LMB (6 mo-3 yr)	< 0.01	< 0.01														
4	LMB (0-6 mo)	< 0.01	< 0.01	< 0.01													
5	black crappie adult																
6	black crappie (0-12 mo)	< 0.01	< 0.01	0.01													
7	bluegill / redear adult	0.01	< 0.01														
8	bluegill / redear (0-12 mo)	0.01	< 0.01	0.04													
9	centrarchid	0.04	0.32	0.20													
10	prey fish	0.37	0.16	0.25	0.40	0.02	0.02										
11	generalist fish	0.20	0.27	0.21	0.11	0.19	0.10										
12	zoobenth fish	0.23	0.21	0.18	0.06	0.10	0.05										
13	grass shrimp	0.03		0.01	0.05	0.01	0.01	0.15	0.12	0.05							
14	ephiphytic invertebrate	0.05		0.04	0.25	0.11	0.16	0.25	0.20	0.30	0.15	0.30	0.10				
15	benthic invertebrate	0.05		< 0.01	0.11	0.32	0.44	0.45	0.44	0.38	0.45	0.20	0.50				
16	zooplankton			0.06	0.03	0.25	0.23	0.15	0.25	0.20	0.38	0.30	0.10				
17	epiphytic algae										0.01	0.10		0.22	0.88		
18	floating leaf																
19	emergent vegegation																
20	native submersed																
21	hydrilla																
22	phytoplankton									0.01							1.00
23	tussock																
24	detritus									0.06	0.01	0.10	0.30	0.78	0.13	1.00	
	Import																
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

sources:
Durant et al. (1979)
published Ecopath models
Rogers and Allen (2005)
Sammons and Maceina (2006)
Schramm et al. (1983)
Tuten et al. (2008)
www.fishbase.org

Table 2-4. Ecosim vulnerability inputs that control flows from invulnerable to vulnerable for prey groups (left column) for each predator (across top row).

Group number	Functional group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	predators		2.5														
2	LMB-adult																
3	LMB (6 mo-3 yr)	1.83	1.83														
4	LMB (0-6 mo)	1.01	1.01	1.01													
5	black crappie adult																
6	black crappie (0-12 mo)	1.8	1.83	1.83													
7	bluegill / redear adult	2	2.5														
8	bluegill / redear (0-12 mo)	1.8	1.8	1.83													
9	centrarchid	2	2.5	1.83													
10	prey fish	2	2.5	1.83	2.64	2.5	1.83										
11	generalist fish	2	2.5	1.83	2.64	2.5	1.83										
12	zoobenth fish	2	2.5	1.83	2.64	2.5	1.83										
13	grass shrimp	2		1.83	2.64	2.5	1.83	4.83	2	2							
14	ephiphytic invertebrate	2		1.83	2.64	2.5	1.83	4.83	2	2	2	2	2				
15	benthic invertebrate	2		1.83	2.64	2.5	1.83	4.83	2	2	2	2	2				
16	zooplankton			1.83	2.64	2.5	1.83	4.83	2	2	2	2	2				
17	epiphytic algae										2	2		2	2		
18	floating leaf																
19	emergent vegegation																
20	native submersed																
21	hydrilla																
22	phytoplankton									2							2
23	tussock																
24	detritus									2	2	2	2	2	2	2	

Table 2-5. Ecospace preferred habitats (x) for functional groups (LMB = largemouth bass). Preferred habitats had higher feeding rates, lower predation mortality, and lower emigration relative to non-preferred habitats.

Group number	Functional group	All	Littoral	Nearshore	Offshore	Tussock
1	predators		x	x	x	
2	LMB-adult		x	x		
3	LMB (6 mo-3 yr)		x	x		
4	LMB (0-6 mo)		x			
5	black crappie adult			x	x	
6	black crappie (0-12 mo)		x	x		
7	bluegill / redear adult		x	x		
8	bluegill / redear (0-12 mo)		x			
9	centrarchid		x			
10	prey fish		x			x
11	generalist fish		x	x		
12	zoobenth fish		x	x	x	
13	grass shrimp		x			x
14	ephiphytic invertebrate		x			x
15	benthic invertebrate	x				
16	zooplankton		x	x	x	
17	epiphytic algae		x			
18	floating leaf		x			
19	emergent vegegation		x			
20	native submersed		x			
21	hydrilla		x			
22	phytoplankton		x	x	x	
23	tussock					x
24	detritus	x				

Table 2-6. Ecosim predicted biomass (kg/ha) and predicted biomass change
(%; relative to no control) immediately after a removal (10-year control)
and at equlibrium for combined controls.

Functional group	Baseline biomass (kg/ha)	No control (kg/ha)	No control (%)	After 10-yr control (%)	Combined controls (%)
predators	66.0	86.1	31	-6	-14
LMB-adult	17.5	9.5	-46	14	41
LMB (6 mo-3 yr)	9.2	5.1	-45	64	44
LMB (0-6 mo)	0.2	0.1	-49	37	52
black crappie adult	5.1	4.4	-14	27	0
black crappie (0-12 mo)	1.0	0.9	-13	9	0
bluegill / redear adult	56.3	30.1	-47	51	34
bluegill / redear (0-12 mo)	3.8	1.6	-57	77	54
centrarchid	44.7	2.2	-95	>100	>100
prey fish	74.4	107.4	44	-19	-13
generalist fish	76.1	80.5	6	2	-3
zoobenth fish	66.0	65.3	-1	5	0
grass shrimp	15.0	45.7	304	-51	-43
ephiphytic invertebrate	164.9	165.6	0.4	2	1
benthic invertebrate	118.3	106.3	-10	11	5
zooplankton	149.2	136.1	-9	7	4
Fishery catches					
largemouth bass	3.2	1.7	-45	14	40
black crappie	2.0	1.7	-14	26	1
bluegill-redear	7.9	4.2	-47	51	34

Table 2-7. Ecospace predicted biomass per area
differences (%) following a simulated restoration
that decreased tussock surface coverage from
 30% to 15%.

| Functional group	% change after restoration
predators	2
LMB-adult	56
LMB (6 mo-3 yr)	-14
LMB (0-6 mo)	16
black crappie adult	81
black crappie (0-12 mo)	61
bluegill / redear adult	>100
bluegill / redear (0-12 mo)	>100
centrarchid	>100
prey fish	-26
generalist fish	15
zoobenth fish	33
grass shrimp	-56
ephiphytic invertebrate	14
benthic invertebrate	17
zooplankton	8
Fishery catches	
largemouth bass	25
black crappie	77
bluegill-redear	>100
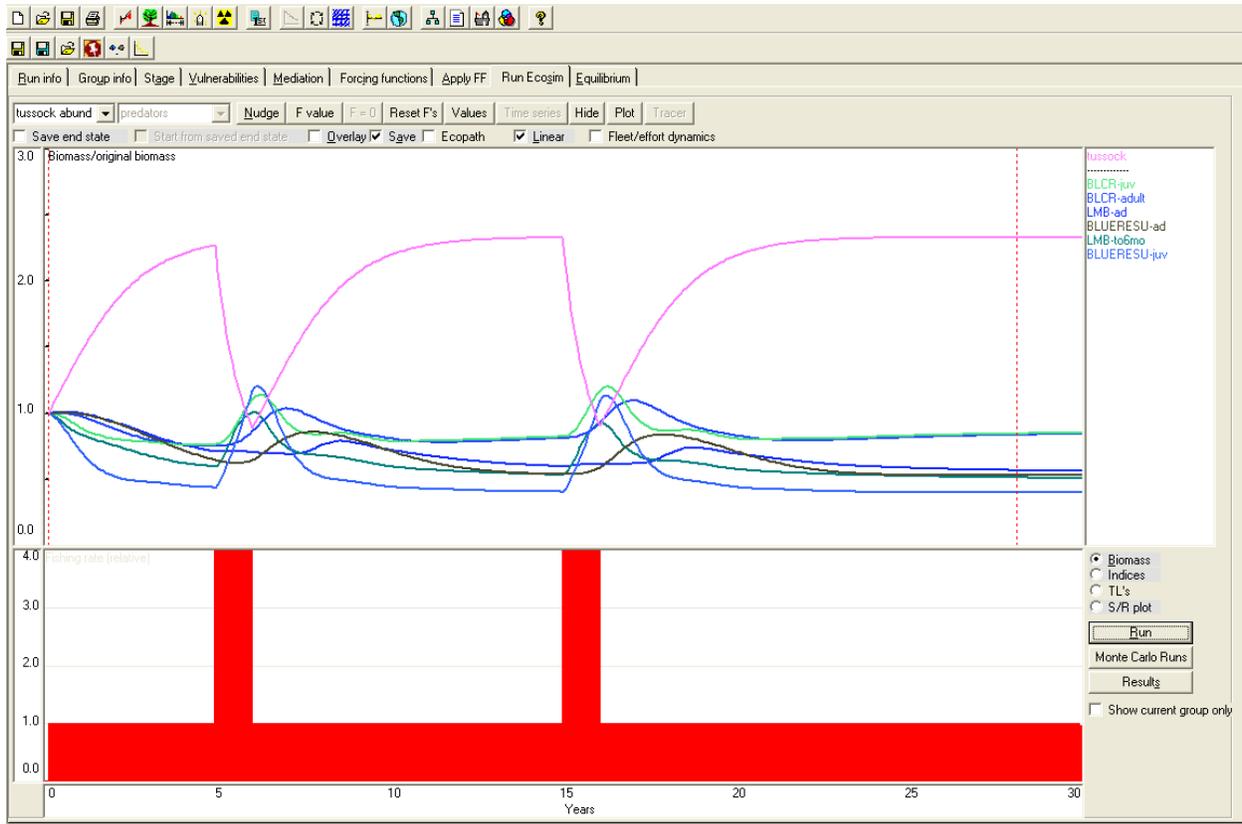
Figure 2-1. Ecosim predicted biomass changes following 10-year tussock control. The top portion shows predicted biomass changes (1.0 = base Ecopath biomasses) and the bottom panel shows simulation year and fishing mortality multiplier (1.0 = base Ecopath fishing mortality). The pink line represents tussock biomass and blue-green lines represent sport fish group biomasses.
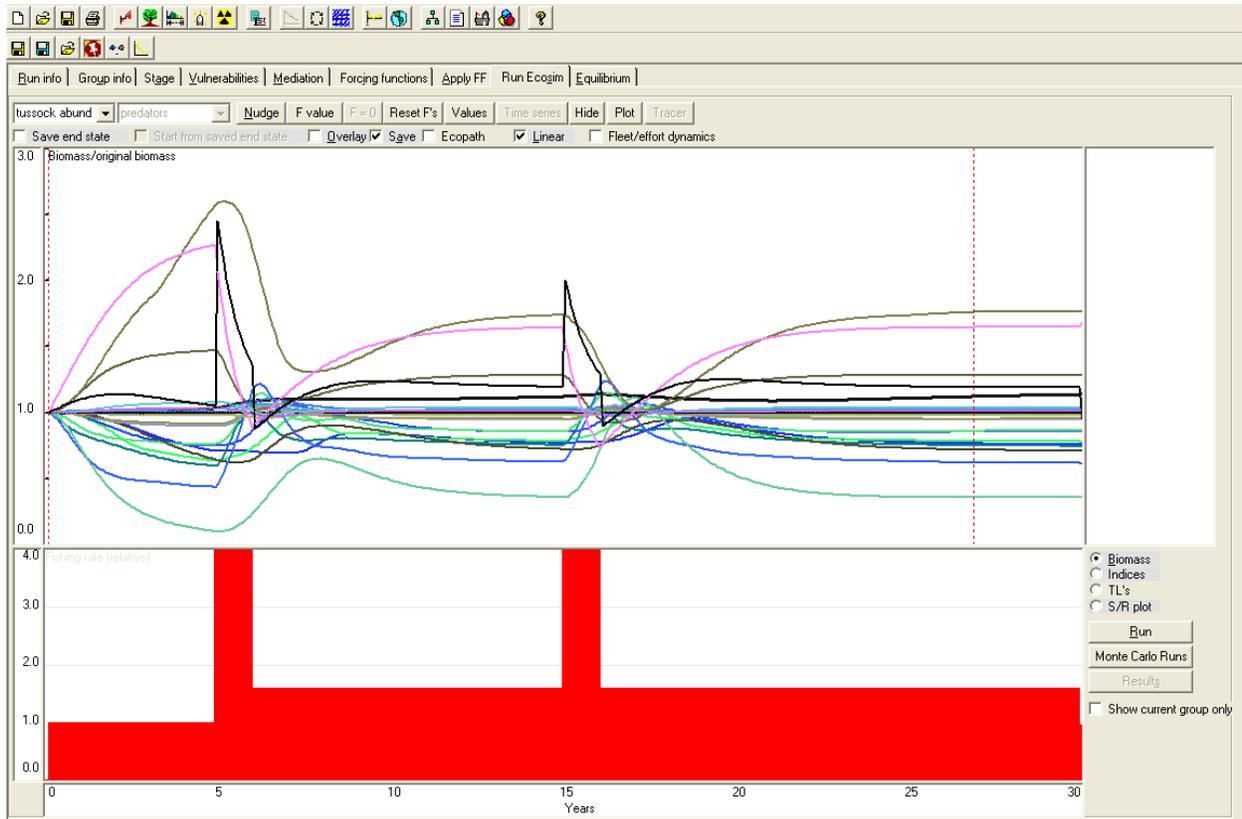
Figure 2-2. Ecosim predicted biomass changes following combined controls (10-year control and maintenance efforts) for tussocks. The top portion shows predicted biomass changes (1.0 = base Ecopath biomasses) and the bottom panel shows simulation year and fishing mortality multiplier (1.0 = base Ecopath fishing mortality). The pink line represents tussock biomass and blue-green lines represent sport fish group biomasses.
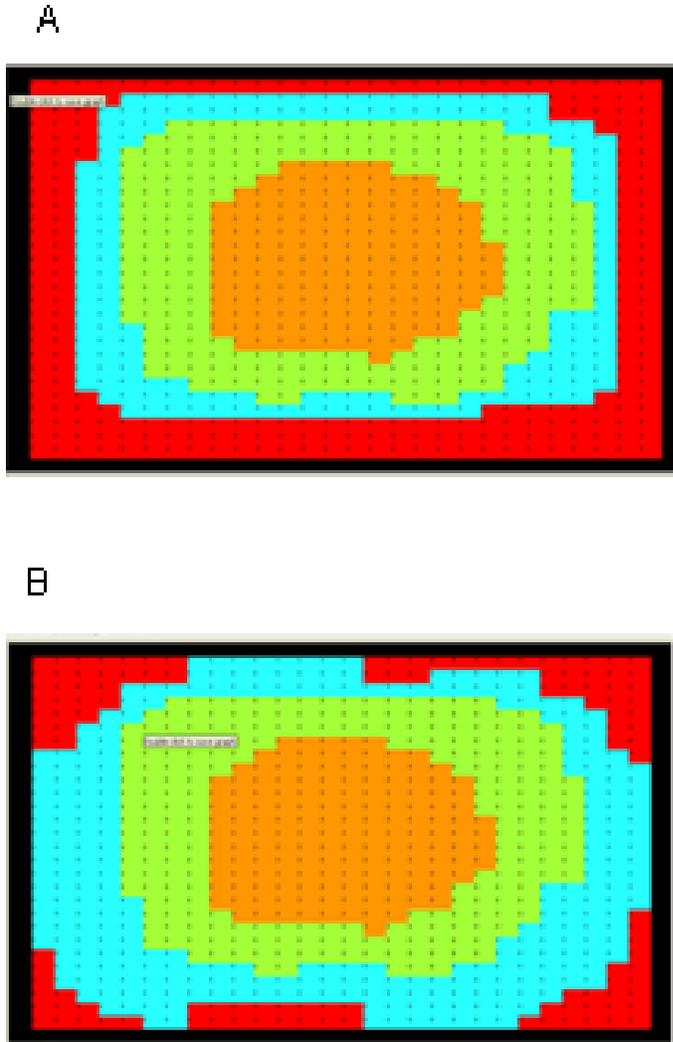
66

A

B

Figure 2-3. Ecospace map showing habitat distributions before (panel A) and after (Panel B) a simulated habitat restoration project that reduced tussock coverage from 30% (panel A) to 15% (panel B). Habitat types are red = tussock, blue = quality littoral, green = nearshore open water, and orange = offshore open water.

DISCUSSION

Ecosystem models exposed trade-offs associated with differing tussock control management options and showed strong influences of littoral habitat composition on fish community distributions and fisheries. Ecosim models indicated that infrequent high intensity removals would not be adequate for maintaining littoral habitats at a suitability equivalent to combined control efforts that included low frequency removals and maintenance herbicide use. The spatial model indicated that restoration projects that reduced spatial coverage of tussocks would provide positive benefits to most sport fish and the fisheries they support. Furthermore, the spatial arrangement of tussock removals could largely affect restoration benefits because edge effects were pronounced.

Our major Ecosim findings showed that combining infrequent (every 10 years) tussock removals with periodic herbicide use to lower the rate of tussock expansion was the best management strategy for confronting negative tussock effects that can result from stabilized water levels. Without any control efforts, the ecosystem was predicted to reach a stable equilibrium with increased predator and prey fish biomasses and decreased sport fish abundance and fishery catches relative to baseline Ecopath conditions. These results were primarily driven by abundance $\times$ diet composition interactions (e.g., fewer largemouth bass preying on juvenile predators) and mediation functions that allowed tussock habitat to provide refugia for prey fish from predators. Low-frequency high mortality events for tussocks allowed for short-lived restoration of littoral areas and allowed for temporary biomass increases for some functional groups, but the system was predicted to return to the same steady-state as implementing no controls within a few years. Adult sport fish standing crops were predicted to increase by $> 25\%$ relative to no control, but infrequent control effects were not stable. Ecosim predictions were

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similar to results at Lake Tohopekaliga, Florida following an intense habitat restoration project

(Moyer et al. 1995). The habitat restoration at Lake Tohopekaliga resulted in a short-lived

immediate impact to sport fish abundance, however restored sites reverted to back to poor

quality habitats dominated by dense emergent macrophytes within three years (Moyer et al.

1995). Although our species groupings precluded exact comparisons with previous restoration

evaluations, our predictions of increased predators with increased tussocks reflected results from

Moyer et al. (1995) that reported high abundance of "rough fish" in unrestored sites.

Thus, Ecosim predicted that combining maintenance controls with intensive removals

would provide the most benefits relative to other policy options. Adult sport fish standing crops

were predicted to be > 30% higher relative to no controls or infrequent controls and these results

were predicted to be long-term. Our results for combined controls suggested that continued

controls would maintain positive benefits, although benefits would be partially reduced relative

to benefits immediately after restoration.

Our spatial ecosystem models that allowed for expansive tussock coverage resulted in

lower biomass for several sport fish groups, localized concentrations for some groups in

remaining preferred habitats, and reduced fishery catches. However, biomass increases were

predicted for functional groups that could utilize tussock habitats. When we allowed tussocks to

dominate the available littoral area (i.e., 30% of total lake surface area), we saw large declines

for most fish species with the exception of our "prey fish" group. Similarly, Bunch et al. (2008)

reported that dense-emergent plant habitats at Lakes Istokpoga and Kissimmee were dominated

by stress-tolerant species (i.e., primarily Cyprinodontidae) and stress-moderate (i.e., included

Centrarchidae taxa) composed only 5% of total catch. Ecospace also predicted large biomass

increases for grass shrimp within tussock habitats due to reduced mortality because predator,

sport fish, and centrarchid biomasses were lower in these areas relative to higher quality habitats. Butler et al. (1992) reported no differences in grass shrimp densities between restored and control sites at Lake Tohopekaliga in the year following a drawdown, but higher densities in restored sites were detected one year later after rapid re-colonization by dense emergent plants.

Our results only partly corresponded to previous field evaluations of lake restoration efforts on sport fish species. For example, Allen and Tugend (2002) and Tugend and Allen (2004) reported that a large scale restoration project "opened up" previously unavailable habitats and control efforts allowed benefits to persist for at least three years following the restoration. This matches our model predictions that removal of tussock habitat improves habitat quality for juvenile sport fish. However, Ecosim also predicted persistent increases in fishery catches for largemouth bass and bluegill-redear fisheries relative to no control (40% and 34%, respectively). No previous studies have shown increases in sport fish catches following lake restoration practices. Allen et al. (2003) showed that electrofishing and angler catch per hour of largemouth bass did not decline after the 1996 restoration effort at Lake Kissimmee, Florida, but fishing effort declined substantially. The Ecosim model indicated that management policies that combined drawdowns and control efforts should be implemented to weaken negative community effects of tussock habitats and improve sport fisheries on a lake-wide scale. To our knowledge no previous habitat restoration projects in Florida have evaluated lake-wide effects of restoration projects, and thus, our predictions are yet to be tested. The strength of our assumptions regarding negative effects of tussock biomass could have under-represented the significance of other habitat types (e.g., emergent vegetation, floating leaf) on fish metrics and potentially overestimated the impacts of tussock removal on a lake-wide scale.

One of the most interesting findings of this study is that the model indicated that edge habitats between tussocks and other littoral habitats could be important at the whole-lake scale and would at least partially offset the impacts of habitat loss from tussock expansions. Thus, simulations indicated a research need to quantify the value of edge habitats and how that value varies with tussock patch size and proximity to more quality habitat (i.e., areas with intermediate plant coverage). Detailed spatial predictions for largemouth bass showed that biomass differed among restored and unrestored sites, but edge effects were also strong. Edge effects could result in two ways: 1) spillover from quality littoral habitat to result in high biomasses along tussock edges, or 2) factors limiting survival are less strong along tussock edges than interior areas. Moyer et al. (2005) reported that most largemouth bass at Lake Tohopekaliga were collected along plant edges when littoral zones were dominated by dense aquatic vegetation. Nonetheless, age-0 largemouth bass biomasses in interior portions of tussock habitat were predicted to be very low compared to quality habitat. Bunch et al. (2008) reported habitat-dependent and fine-scale variation in water quality within dense emergent plant stands that could provide local refugia from anoxic conditions, but dissolved oxygen levels were generally higher near openwater-vegetated interfaces. Thus, our simulations appeared to capture the major fish community-tussock habitat dynamics and prediction directions reflected results of habitat restoration field projects.

Results from Ecospace also illustrated the difficulty in detecting biomass differences between restored and unrestored sites. Although mean biomass was significantly lower in unrestored sites than restored sites when edges were not sampled, variability in sampling gears would likely preclude the ability to detect differences unless sampling locations had very clear habitat contrasts (i.e., quality littoral habitat versus interior tussock habitat). For example,

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Tugend (1999) reported that mean fish biomass coefficients of variation ranged from 54-150% using 0.08 ha block nets in restored sites at Lake Kissimmee, Florida (also see Chapter 1). Furthermore, plant densities within interior tussock habitats create challenges to quantitatively comparing restored and unrestored habitats as described in previous evaluations (e.g., Allen and Tugend 2002).

Our Ecopath model and Ecosim/Ecospace simulations should be considered hypothetical representations of a large Florida eutrophic lake. Havens et al. (1996) reported that > 10,000 trophic linkages existed within Lake Okeechobee, and therefore, capturing the full extent of predator-prey dynamics is impossible. Thus, our model could not predict all individual fish species responses that may be evident in field studies. For example, Wegener and Williams (1975) and Tugend and Allen (2004) reported that Seminole killifish *Fundulus seminolis* biomass and catch were much higher in restored littoral sites than in tussock dominated sites following restorations. They suggested that this was caused by higher quality habitat due to sandy substrate preferences for this species. However, it would be very challenging to derive similar species-specific predictions from EwE models because diet data are often not available at a fine enough scale to inform diet inputs, detailed life-history data are often unavailable to inform habitat-dependent survival, and biomass of many species (e.g., small bodied) is difficult to estimate.

Specified fish-habitat relationships and mediation factors suggested areas for further research and model exploration. Specific considerations for our Ecosim assumptions that possibly vary among waterbodies include: 1) strength and shape of mediation effects, 2) difficulties relating biomass per area to spatial coverage, and 3) rate of tussock biomass accumulation. For example, tussock habitat accumulation would depend on plant colonization

and growth rates that would vary with wind and wave action (e.g., lake size), nutrient availability, and water depth (Keddy 1983). Specific considerations for our Ecospace assumptions that possibly vary among waterbodies include: 1) assignment of functional groups to preferred habitats, 2) determining relative performance among habitats, and 3) spatial structuring of habitats within simulations. For example, Conrow et al. (1990) reported that several fish species use different and multiple vegetated habitats during their life stages. Thus, developing fine-scale habitat-dependent spatial models and accounting for ecological interactions within each would be very challenging. Also, the prominence of edge effects, influence of habitat distribution mapping, and functional group movement rate inputs were important for fish distribution predictions. Thus, spatial ecosystem model development involves challenges comparable to exercises attempting to model marine protected areas. Fortunately, the flexibility of EwE software allows for exploration of how strongly user inputs and assumptions affect predictions. For example, our simulations indicated that modeling large contiguous restoration areas would have larger effects on predictions than modeling many small restoration patches. Thus, the potential for edge effects to mitigate against the quantity of tussock habitats was dependent on the proximity to large expanses of quality habitats that facilitated high standing crops. Refining ecosystem models will require future field projects (e.g., measuring juvenile fish movements) and experimental data (e.g., variation in prey vulnerability across habitat type and density) to better inform model inputs and assumptions.

In summary, our EwE model exhibited the ability to capture the general ecosystem dynamics for a large, eutrophic Florida lake and a simulation tool for evaluating potential outcomes of proposed habitat management projects. Our modeling exercise also illustrated data gaps that offer opportunities to refine model inputs. The model's sensitivity to diet composition

inputs and the importance of the grass shrimp functional group implied that these are key areas for further work. For example, grass shrimp biomass and predator vulnerability played a strong role in ecosystem trophic dynamics and functional group responses because they were a common prey item across multiple functional groups. Although Essington (2007) showed that Ecopath inputs were more sensitive to B and P/B inputs than to diet composition data, he also concluded that "bad data led to bad predictions." Thus, our ecosystem model should be considered a starting point that evolves via a cooperative working group that seeks to reduce model uncertainty and continues model development. For example, the developing EwE version 6 will allow users to map habitat-specific salinities and functional group salinity tolerances that could be implemented to represent dissolved oxygen concentrations, and thus, influence habitat use. The model could also be expanded to incorporate other species (e.g., wading birds, alligators *Alligator mississippiensis*) that are important to resource management policy considerations. Future model exploration and data collection that exposes trophic dynamics and habitat-dependent ecological interactions will be critical in determining the usefulness of ecosystem models for habitat management in large Florida lakes.

Implementing large-scale habitat restoration projects at large Florida lakes will be challenging in the future due to economic, environmental, and social constraints. Therefore, determining the value and necessity for habitat restoration projects will require science-based information that provides a system-wide ecological perspective on the costs and benefits expected. A significant future study need is to evaluate habitat edge effects across the mosaic of littoral areas where they exist. No previous field studies have measured how edge habitats, and their proximity to high-quality habitat areas influence bird, reptile, and fish community composition and abundance. This approach would complement previous studies that have

reported within and among habitat comparisons of fish communities by providing information on how surrounding areas affect habitat suitability. Previous studies have worked on a relatively small scale within habitat patches (e.g., Allen and Tugend 2002), but there is a need to evaluate habitat quality at a broader scale that considers the value of local habitat conditions while considering the larger mosaic in which they exist. Studies of this type will require sampling designs paired with GIS maps to evaluate habitat quality at broader scales. Manipulative experiments should also be considered to provide insight into habitat-dependent trade-offs that influence prey availability and survival to identify mechanisms structuring habitat suitability. In conclusion, field studies and experiments will be required for fully exposing fish community and habitat relationships. However, ecosystem models such as those developed in this study can provide a framework for a science-based approach to setting goals and evaluating success of lake restoration efforts in Florida.

Acknowledgments

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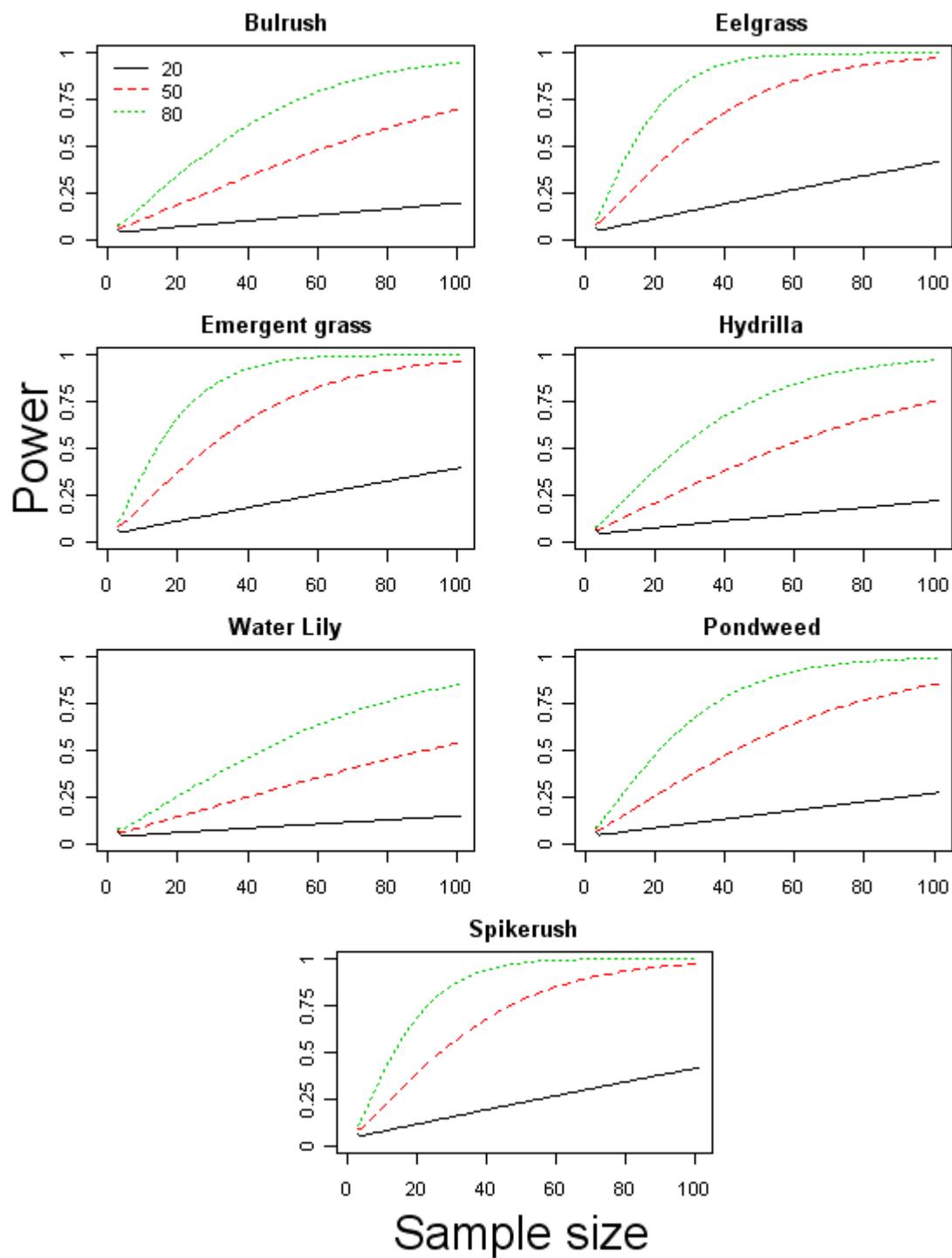
Appendix I: Power to detect habitat-specific sport fish and functional group abundance changes in 0.08 ha block nets
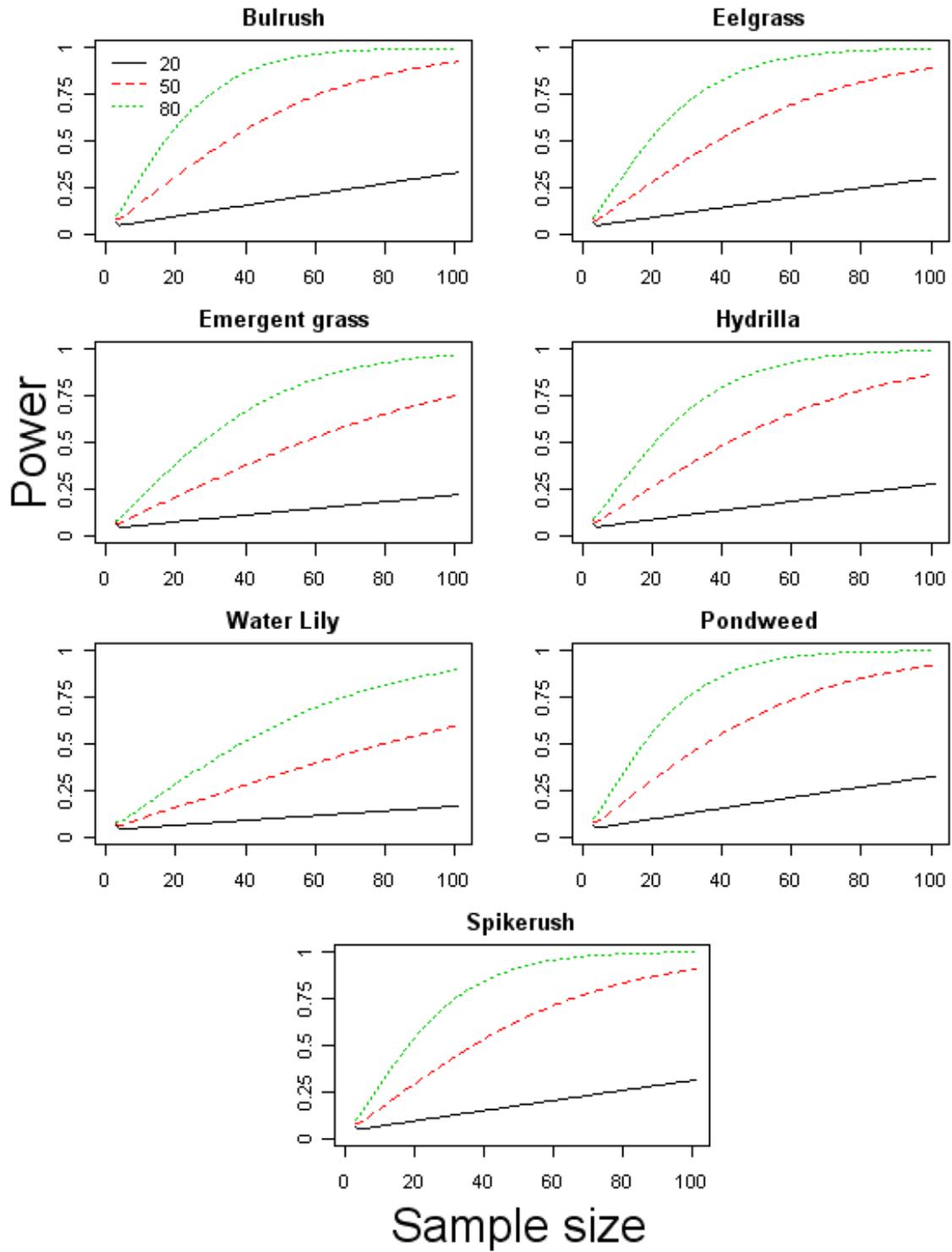
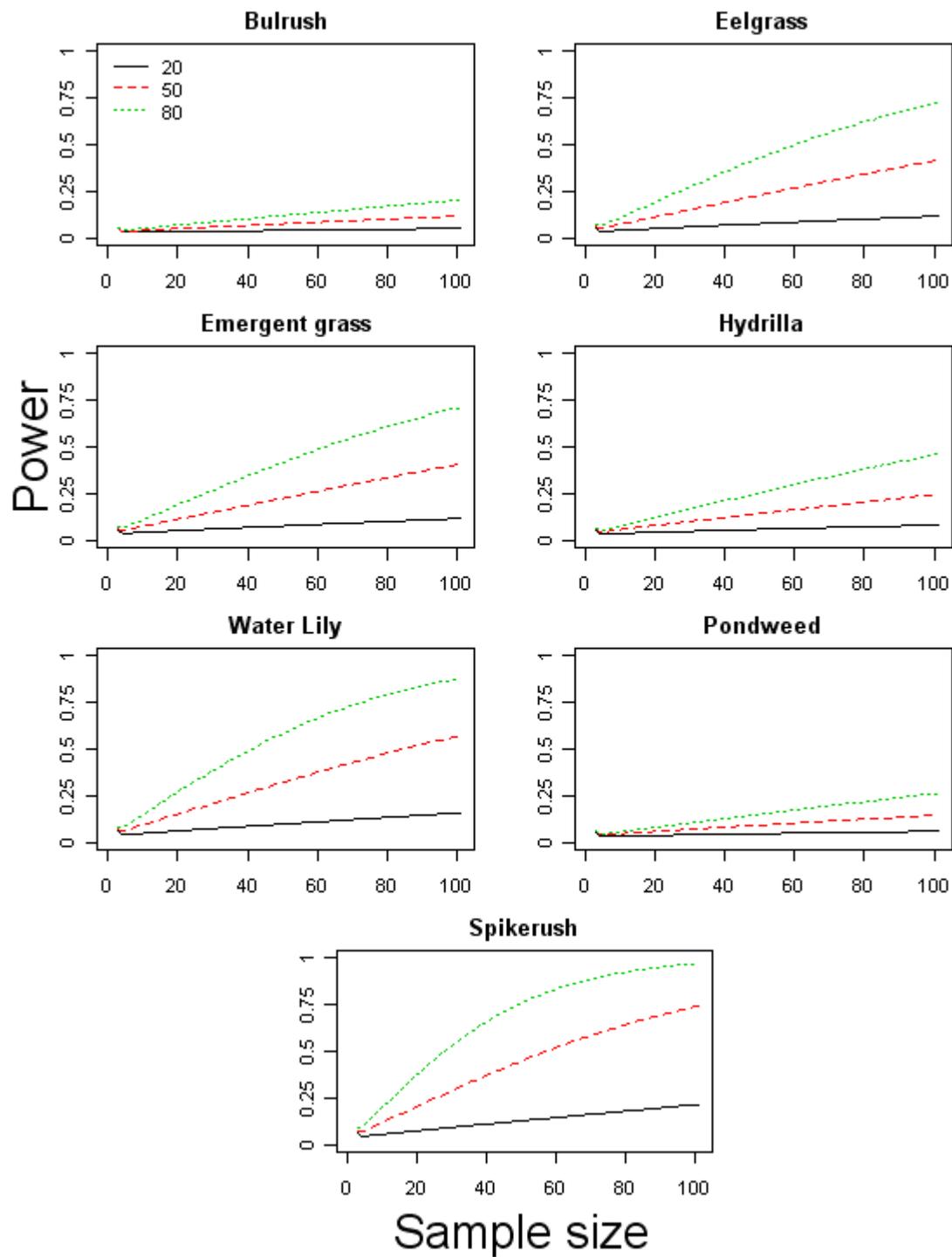Black crappie abundance in 0.08 ha blocknets

Power
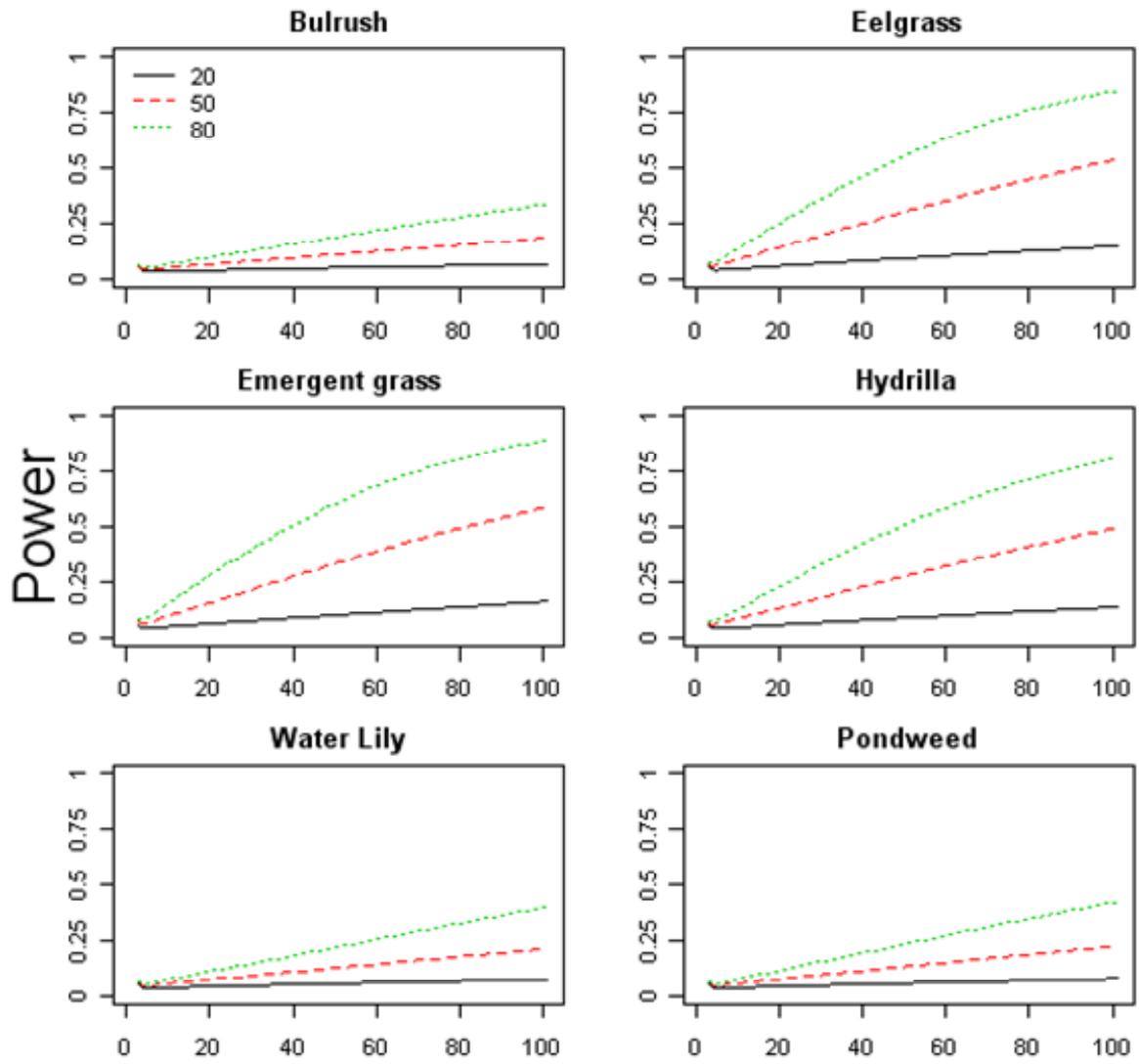
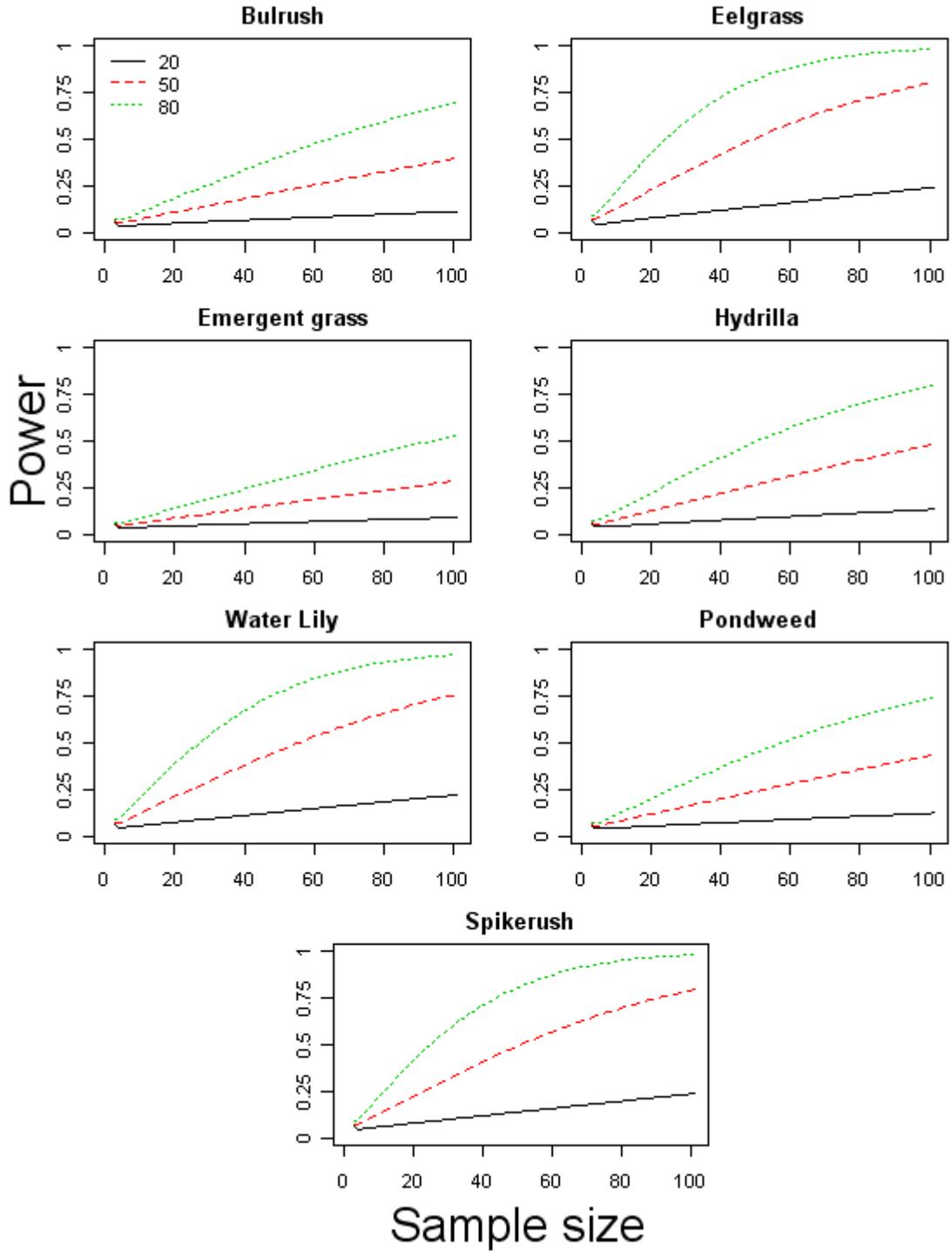Sample size

Largemouth bass abundance in 0.08 ha blocknets

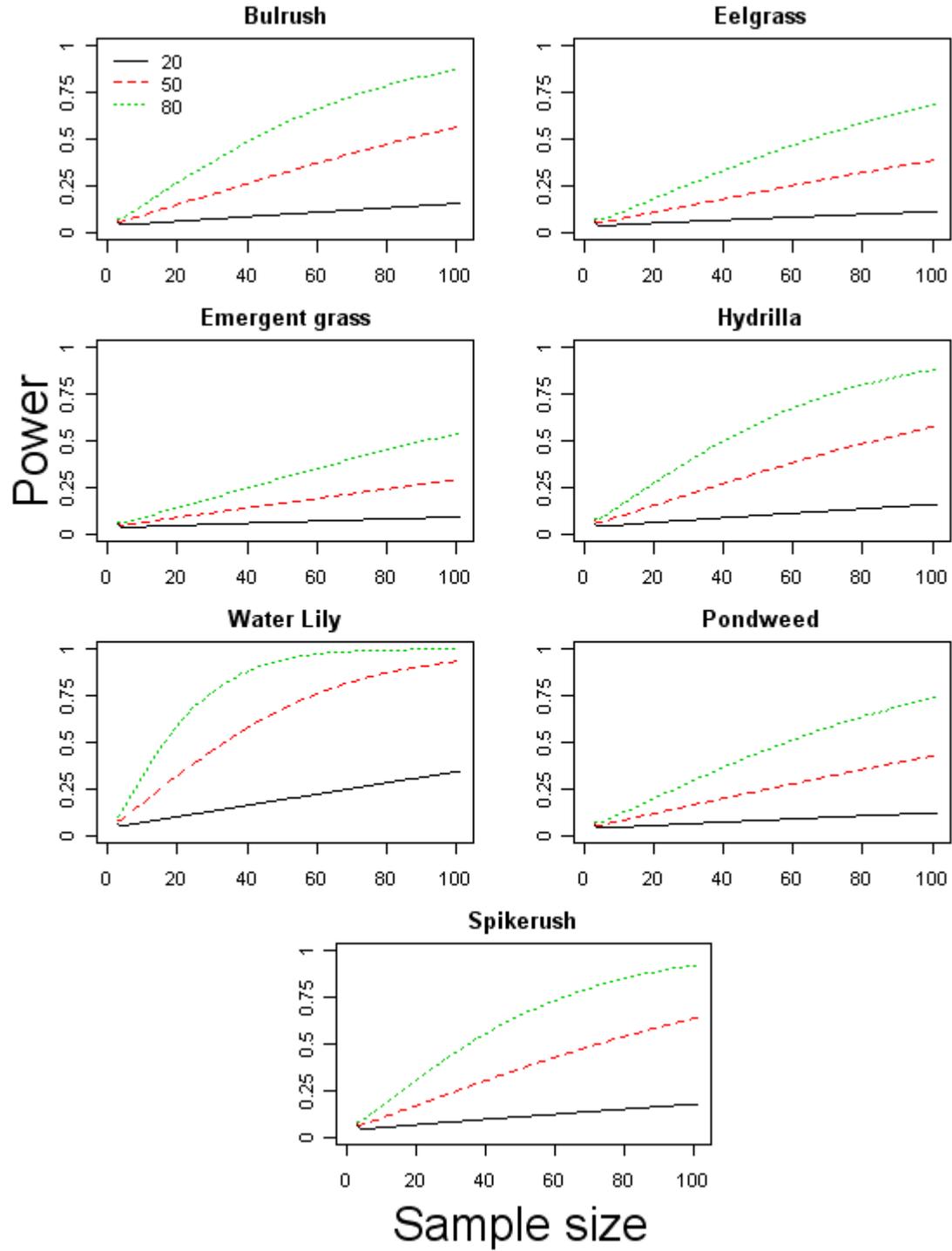**Bluegill and redear sunfish abundance in 0.08 ha blocknets**

Generalist abundance in 0.08 ha blocknets

Predator abundance in 0.08 ha blocknets

Prey abundance in 0.08 ha blocknets

Zoobenthivorous abundance in 0.08 ha blocknets