HABITAT MEDIATED COMMUNITY STRUCTURE WITHIN SPRING-FED, COASTAL RIVERS

By

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Equation Variables and Parameters

A	Sample area
B	Population biomass
C	Number of captures per sample
D	Population density
E	Sample effort
LL	Log-likelihood
LN	Natural logarithm
M	Number of marked individuals
MW	Mean prey proportion by dry weight
MWB	Mean prey dry weight per predator body weight
N	Population abundance
p	Probability of capture
q	Catchability coefficient
R	Number of recaptured individuals
w	Average weight per individual

Water Quality Variables

ALK	Alkalinity measured as calcium carbonate
NO3	Nitrate
SAL	Salinity
SAV	Submersed aquatic vegetation (macrophytes and filamentous algae combined)
SRP	Soluble reactive phosphorus
TEMP	Temperature

Abstract of Dissertation Presented to the Graduate School
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Vegetation plays a central role in structuring aquatic ecosystems by altering biogeochemical processes and mediating trophic interactions between fishes and invertebrates. The loss of key vegetative habitat components can alter community structure, and lead to the loss of ecosystem function and services. The goal of this study was to quantitatively assess the effects of macrophyte loss on fish and invertebrate populations within spring-fed, coastal rivers. To accomplish this, I conducted a comparative ecosystem study of two rivers, the Chassahowitzka and Homosassa rivers, where vegetation loss has been disparate over the last 12 years.

I sampled aquatic vegetation, invertebrates, and fishes in each river over a three-year period to estimate the community composition and biomass, and examined the diet habits of freshwater and marine fishes. Using empirically derived estimates of community biomass and trophic interactions, I constructed a trophic mass-balance model of the Chassahowitzka River food web and ran time-dynamic simulations to predict the response of fish and invertebrate populations to the extirpation of macrophytes. I compared predicted estimates with the observed community structure

of the Homosassa River, where macrophytes have been absent for nearly a decade. Overall, macrophyte extirpation was predicted to result in a 60% reduction in invertebrate biomass and 11% reduction in fish biomass, whereas restoration was predicted to increase invertebrate biomass by 152% and fish biomass by 73%. Observed spatial patterns between rivers validated model predictions for most taxa, including the local extinction of select freshwater groups.

This research exemplified the complex trophic interactions that structure aquatic food webs. As vegetative communities shift from highly-structured macrophyte dominated assemblages to boom-and-bust filamentous algae production, an associated shift in primary and secondary food bases is expected to have compound effects on predator populations, including altered prey composition and population dynamics. Predators that forage on a wide range of fish and invertebrate taxa are likely to switch dominant prey types, while specialist species may decline or, in extreme cases, be extirpated from the system. The long-term ecological and socioeconomic consequences of the predicted changes in community structure of coastal river ecosystems remain unknown.

CHAPTER 1
GENERAL INTRODUCTION

Introduction

Habitat loss is a principal cause of species decline and imperilment (Wilcox and Murphy 1985), and a significant factor contributing to the global reduction in biodiversity (Fahrig 1997, 2003). Direct effects of habitat loss on animals include lowered breeding success, dispersal, foraging success, and survival (Fahrig 2003). These direct effects, in turn, influence species-level population dynamics that can ultimately affect entire communities. Indirect effects of habitat loss on communities occur primarily as a consequence of altered trophic interactions among populations (Taylor and Merriam 1995). For example, a reduction in habitat complexity associated with the loss of habitat (e.g., macrophyte extirpation, river channelization, deforestation) can increase predation vulnerability and mortality of prey species (Crowder and Cooper 1982, Power et al. 1996, Becker et al. 2009), and result in depletion of prey resources followed by subsequent predator population crashes (Huffaker 1958, Hastings 1977, Sutherland and Dolman 1994). The combination of refuge, foraging, and reproductive habitat loss reduces the number of specialist species in a community (Munday 2004) and shortens food chain length (Power et al. 1996, Komonen et al. 2000). In combination, the direct and indirect effects of habitat loss can alter community and food web structure (Harrison and Bruna 1999, Coll et al. 2011), with negative consequences on ecosystems and the services that they provide (Dobson et al. 2006). Quantifying the relationship between key habitat components and populations of animals is essential to predicting (and potentially mitigating) negative species- and community-level responses to large-scale changes in habitat.

Macrophytes are a dominant structural element in many freshwater and coastal ecosystems, and play a key role in a number of biogeochemical and ecological processes (Carpenter and Lodge 1986, Jeppesen et al. 1998). Plants alter the physical and chemical conditions of the water and sediment; influence nutrient cycling, primary production, and the processing of organic matter; and mediate biotic interactions (Jeppesen et al. 1998). As a result of their high productivity and structural complexity, vegetative habitats support a relatively high abundance and diversity of fishes and invertebrates compared to alternative habitats (e.g., Heck et al. 1995, Randall et al. 1996, West and King 1996, Guidetti 2000). Many freshwater and marine fishes and invertebrates utilize vegetative habitats at various phases of their life cycles. For example, seagrass communities along coastlines provide important juvenile rearing habitat for marine fishes and invertebrates, including stocks that support economically important fisheries, such as red drum (*Sciaenops ocellatus*), spotted seatrout (*Mycteroperca microlepis*), and blue crab (*Callinectes sapidus*) (Stunz et al. 2002, Heck et al. 2003, Neahr et al. 2010, Mizerek et al. 2011). Despite the large amount of research dedicated to identifying the role of aquatic vegetation in mediating ecosystem processes, considerably less quantitative research has been applied towards understanding the dynamics between vegetative habitat composition and faunal community structure.

Changes in the physical and chemical properties of the aquatic environment can lead to large-scale shifts in the composition of primary producers, with subsequent effects on food webs (Deegan et al. 2002). For example, eutrophication-driven shifts in the composition of plants and algae may result in the replacement of macrophytes with benthic algae or phytoplankton (Duarte 1995), and potentially alter species interactions and population dynamics (Bettoli et al. 1992, Deegan et al. 2002). Changes in aquatic vegetation can affect trophic interactions by altering refuge and foraging habitat for associated faunal organisms (Gotceitas and Colgan 1989, Heck and Crowder 1991). Aquatic vegetation has been shown to inhibit predator foraging (Crowder and Cooper 1982, Savino and Stein 1982), thereby creating refugia for prey species (Gotceitas and Colgan 1989). Conversely, decreased vegetative cover may increase predation mortality and impact the structure of prey populations (Bettoli et al. 1992). Declines in vegetation composition and biomass can further impact the food base of fishes via competitive exclusion of species (Peterson et al. 1993) and decreased juvenile rearing habitat (Sass et al. 2006). These factors can, in turn, influence population dynamics (Peterson et al. 1993, Richardson et al. 1998) and species interactions with potential community-level consequences (Crowder and Cooper 1982, He and Kitchell 1990, Bettoli et al 1992).

Spring-fed rivers in Florida serve as model ecosystems to study the role that primary producers play in structuring faunal communities. Springs in Florida have long-been recognized as optimal systems for ecological study due to their relatively stable physical and chemical properties; abundant aquatic vegetation, fish and invertebrate communities; and high rates of primary productivity (Odum 1953, Odum 1957). Historically, spring-fed rivers, including the Chassahowitzka and Homosassa rivers, supported dense assemblages of macrophytes, such as *Vallisneria americana*, *Sagittaria kurziana*, and *Potamogeton* spp. Over the last decade, however, a precipitous decline in vegetation biomass has been documented in these systems

(Frazer et al. 2006). The loss of rooted aquatic vegetation, which provides forage and refuge habitat, is likely to alter predator-prey dynamics and other important species-level interactions (Crowder and Cooper 1982). Such alterations may lead to undesirable shifts in fish and invertebrate community composition and possibly the loss of key species (Pillay et al. 2010, Nakamura 2010). Due to the relatively stable abiotic conditions and long-term datasets on vegetation composition and biomass, spring-fed rivers in Florida provide a unique opportunity to study how habitat (submersed aquatic vegetation) mediates the composition and trophic dynamics of faunal groups, and ultimately influences ecosystem structure and function.

The research carried out and described herein allowed for an evaluation of the effects of changes in submersed aquatic vegetation and resulting loss of structural habitat (extirpation of macrophytes and replacement with filamentous macroalgae) on invertebrate and fish community composition and trophic interactions within spring-fed, coastal rivers in Florida. A comparative ecosystem study of two spring-fed rivers along the Gulf of Mexico coast (Figure 1-1) was conducted, and a trophic mass-balance model was developed based on empirically derived estimates of key population-level parameters and predator-prey associations within the Chassahowitzka River. The time-dynamic trophic model was used to predict the effects of macrophyte extirpation on fish and invertebrate community composition, biomass and trophic dynamics. The predictions were compared with the observed community structure of the Homosassa River, where macrophytes have been nearly extirpated for the last decade. Both study rivers are located within close proximity of each other and maintain relatively similar hydrological and chemical properties (Figure 1-2). Prior to the last decade, these systems supported dense communities of macrophytes, fishes and invertebrates (Herald and Strickland 1949, Odum 1953, Frazer et al. 2006). In their current state, however, only one (the Chassahowitzka River) retains any historical semblance of its former plant community (Figure 1-3). The other (the Homosassa River) has an altered vegetation community due to the extirpation of aquatic macrophytes (Frazer et al. 2006). Ecosystem responses to the change in vegetative habitat, as measured by changes in fish and invertebrate communities and the predator-prey interactions within each river were quantitatively assessed. This study comprised 4 study objectives, each of which is addressed subsequently in Chapters 2-5, followed by a summary and synthesis of findings in Chapter 6.

Study Objectives

Objective 1. Estimate the catchability of fishes and invertebrates to standardized sampling gears targeting large-bodied fishes, small-bodied fishes and invertebrates, and evaluate the spatial, temporal and interspecific heterogeneity in gear catchability.

Objective 2. Quantify the composition and biomass of fish and invertebrate assemblages within the Chassahowitzka and Homosassa rivers seasonally and across years in conjunction with the long-term water quality and submersed aquatic vegetation monitoring programs.

Objective 3. Estimate the prey composition, prey selectivity, and relative foraging success of freshwater and marine fishes within the Chassahowitzka and Homosassa rivers.

Objective 4. Quantitatively assess vegetative habitat loss effects on fish and invertebrate community structure using a time-dynamic, trophic mass-balance model, and evaluate model predictions through spatial and temporal comparisons of the observed aquatic communities within the Chassahowitzka and Homosassa rivers.

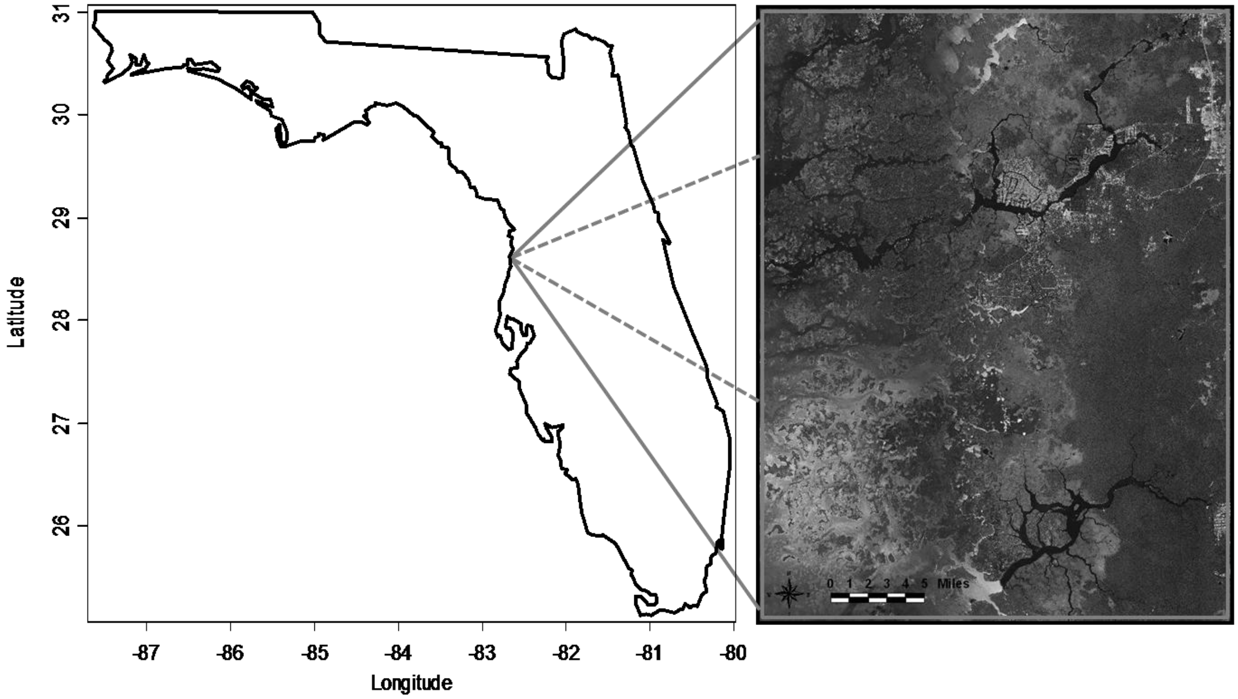

Figure 1-1. Location of the Chassahowitzka (south) and Homosassa (north) rivers in Hernando and Citrus counties, Florida.

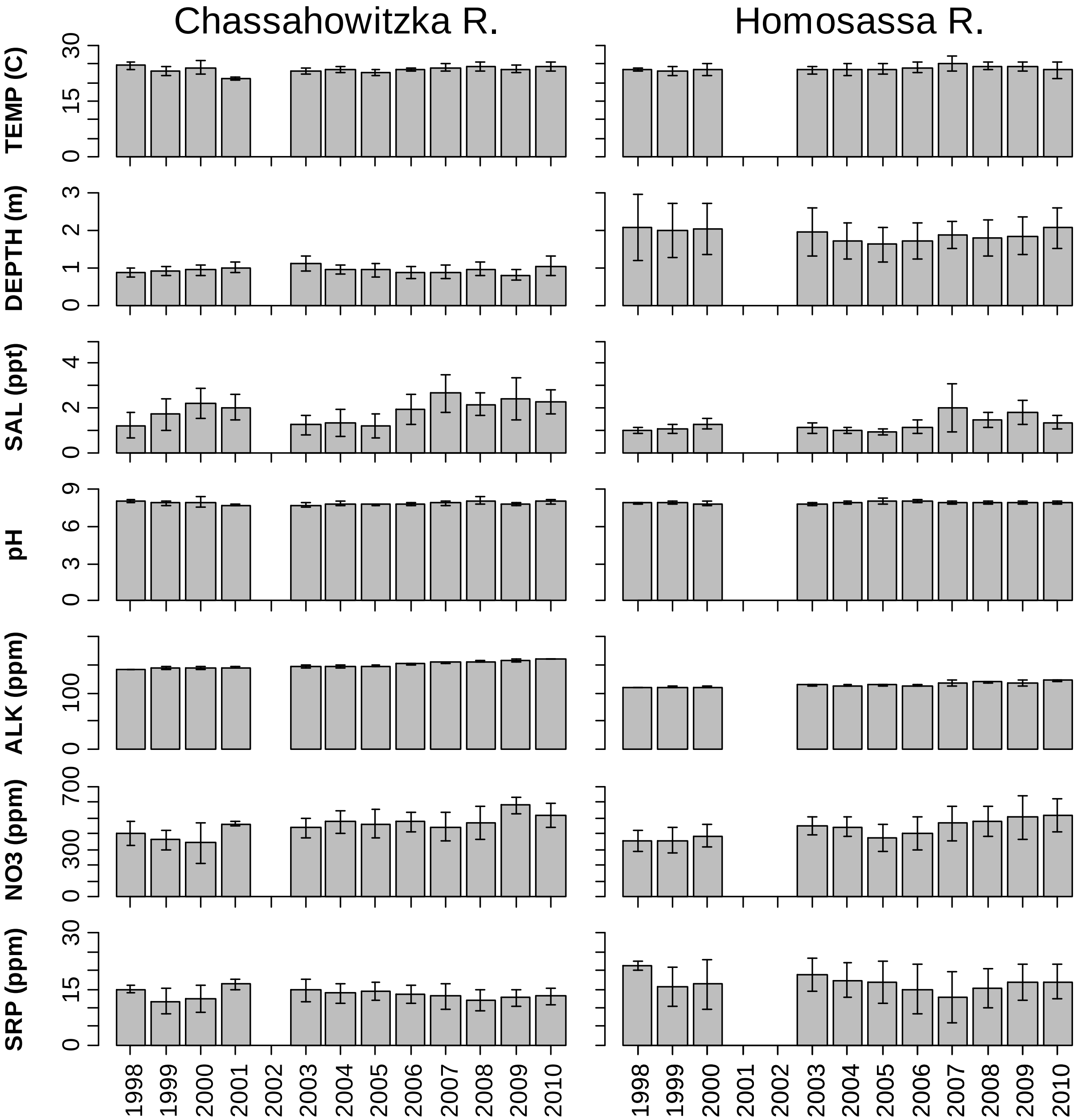

Figure 1-2. Physical and chemical characteristics of the Chassahowitzka and Homosassa rivers between 1998 and 2010 (Frazer, unpublished data). Data represent annual mean values based on quarterly sampling along 10 transects in each system (Frazer et al. 2006).

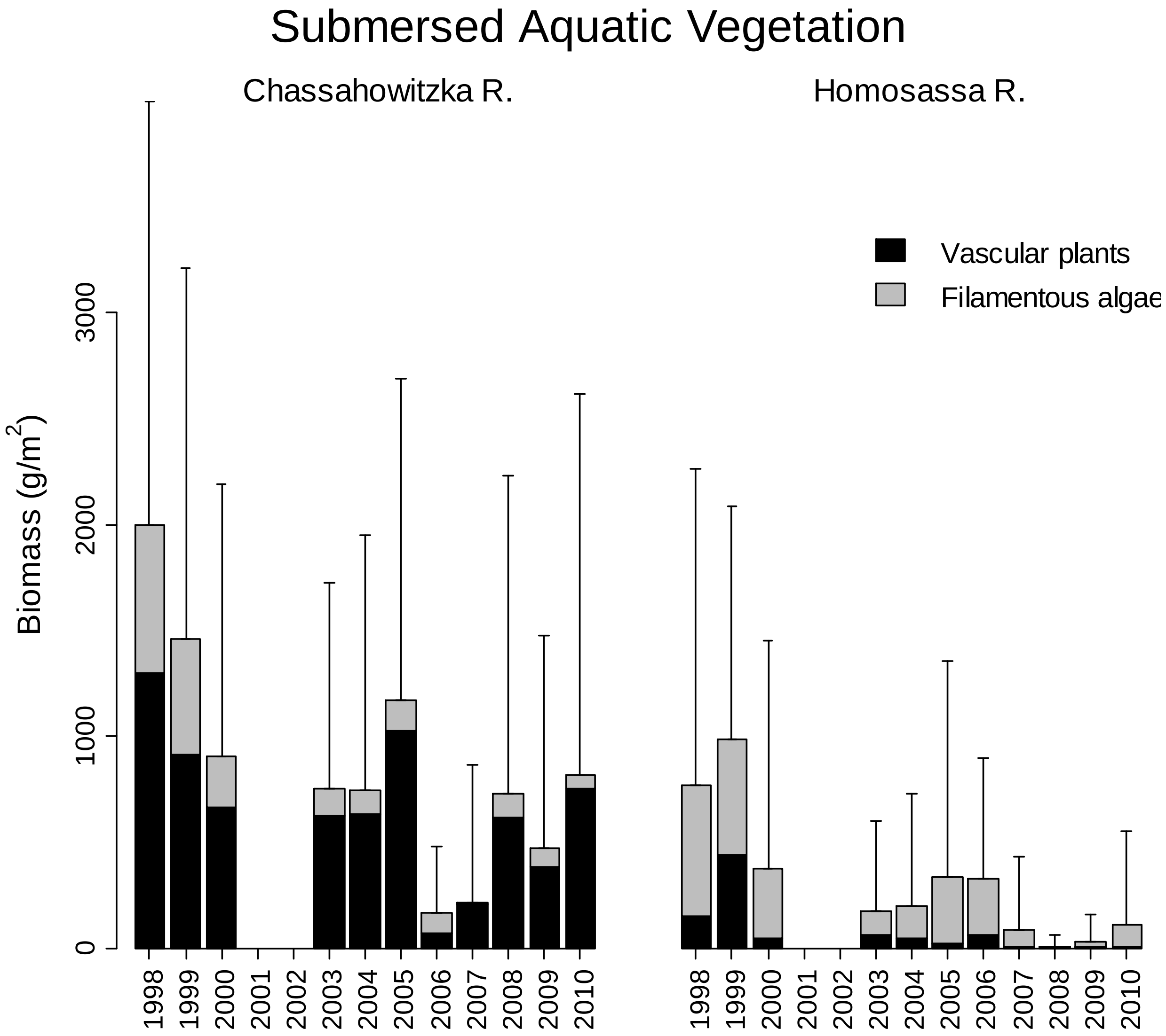

Figure 1-3. Long-term patterns in submersed aquatic vegetation biomass within the Chassahowitzka and Homosassa rivers, Florida.

CHAPTER 2
GEAR CATCHABILITY OF FISHES AND INVERTEBRATES IN COASTAL RIVERS

Introduction

Accurate assessment of fish and invertebrate communities requires information on how population indices generated from disparate sampling methods and gears reflect the ecosystem in terms of absolute abundance, composition and biomass (Nichols 1992, Anderson 2001). Estimation of the capture probability (*p*) of organisms, defined as the probability of capturing an individual within a population during sampling (equivalent to the proportion of the population in the study area captured), is important in characterizing the most basic aspects of community structure, including composition and biomass. While sampling program design and considerations for estimating *p* are widespread in the sampling literature (Pollock et al. 2002, Seber 2002, Williams et al. 2002), incorporating estimates of *p* into the quantitative assessment of aquatic communities has emerged only recently as an area of research focus (e.g., Shea and Peterson 2007, Dauwalter et al. 2008, McCargo and Peterson 2010).

Two components of sampling design should be considered when estimating the *p* of populations to sampling gears, sampling intensity (i.e. amount of sampling effort applied to a study area) and spatial distribution of effort (i.e. number and location of samples relative to the study area). Strong biases in estimates of abundance can result from changes in effort (making animals more or less likely to be captured) or from differences in the distribution of samples (e.g., changes in the proportion of study area sampled). Monitoring programs seeking to characterize community composition should account for variable sampling intensity, as well as spatial and temporal heterogeneity in *p*, for each population of interest.

The density catchability equation (Hilborn and Walters 1992, Pollock et al. 2002) is a linear model that directly relates relative abundance (catch per unit of sampling effort) to population density through a catchability coefficient (*q*). This model can be utilized to effectively incorporate sampling effort and study area into the estimation of *p* and absolute density. By definition, *q* is equal to the ratio of the relative abundance to the absolute density of the population. Frequently in the analysis of fisheries data, *q* is modeled as the ratio of relative abundance to population abundance (e.g., Richards and Schnute 1986, Wang 1999) or biomass (Hilborn and Walters 1992); however, the density catchability model accounts for differences in the units of effort between sampling gears and effectively scales relative abundance indices to a common metric, absolute density (i.e. population abundance estimates are scaled by sample areas to compare across gear types). Application of this modeling framework allows for density to be estimated for multiple populations across trophic levels by deploying several gears that target various guilds within the aquatic community. Theoretically, if *q* is constant and known for each organism detected in the study area, then community composition can be accurately estimated from catch and effort data when adequate samples are taken.

I utilized the density catchability assessment framework to estimate the community composition of fishes and invertebrates within the Chassahowitzka and Homosassa rivers, Florida. My objectives were to estimate the catchability of fishes and invertebrates commonly detected using multiple standard sampling gears (boat electrofishing, seining and throw trap sampling), and to assess the spatial, temporal, and interspecific heterogeneity in catchability estimates. To accomplish this, I implemented capture-recapture and removal sampling to couple relative abundance indices with absolute density estimates. This assessment exemplified the utility of estimating *q* for multiple populations to scale sample indices to estimates of absolute density and obtain measures of community composition. I discuss how this information can be useful for informing the design of ecosystem-based assessments and improving the management and restoration of populations and communities.

Methods

To estimate the relative abundances (catch per unit effort in number of fish per hour electrofishing) and absolute densities (number of fish per km^2) of large-bodied fishes, a team of six crew members implemented multi-pass capture-recapture electrofishing in each study reach during July 2007, January 2008, July 2008 and January 2009. Shoreline and mid-stream transects were sampled once per day for three consecutive days with boat-mounted Smith-Root 9.0 generator powered pulsed electrofishers with output settings ranging between 170 and 340 volts and between 20 and 50 amps. The electrode arrays consisted of stainless steel cathode cables mounted across the bow of the boat and two insulated booms with removable stainless steel cable anode arrays mounted at each corner of the bow on rotating clutches. Shoreline transects included the entire north and south stream banks within a study reach, and transects were sampled from the upstream end of the reach to the downstream end. Mid-stream transects were located at the upper reach boundary, middle of the reach, and lower reach boundary. During electrofishing transects, two people stood on the bow of the boat and dip-netted stunned fish. All captured fishes greater than 150 mm in total length (TL) were tagged in the dorsal fin pterygiophores with a t-bar anchored external tag containing a unique identification number and released along the shoreline in the center of the reach. All fishes greater than 50 mm TL received a batch mark by clipping the terminal end of the left pelvic fin, which created a secondary mark for fishes greater than 150 mm TL.

To examine tag loss and handling mortality, a pilot study was conducted in the Santa Fe River, Florida where 60 fish were held in two replicate pens for three nights. Each pen contained 10 largemouth bass (*Micropterus salmoides*), 10 *Lepomis* spp., and 10 lake chubsucker (*Erimyzon sucetta)* or spotted sucker (*Minytrema melanops*) to estimate tag loss and examine mortality of tagged fish in a confined environment. The observed mortality was expected to be greater than the mortality of handled fish released into the study reaches due to potentially higher predator encounter rates and increased stress on prey species confined with predators.

To estimate the capture probability and absolute density (number of fish per 200 m^2 site area) of small-bodied fishes, a crew of four conducted multiple-pass removal seine depletions at three locations in each study reach during August 2007, February 2008, August 2008 and February 2009. Site locations in each reach included the north river bank, mid-stream and south river bank. Site locations were assigned randomly without replacement to a corresponding electrofishing mid-stream transect, so that both banks and one mid-stream site were sampled per reach. Sites measured 10 m in width by 20 m in length. To ensure closure of the sampling sites to migration, a 60-m block net was set around the perimeter of each site prior to seining. To set the block net, one person guided the boat around the perimeter of the site, while a second person carefully deployed the net over the side of the boat, and a third person secured the net to the stream bottom by placing concrete anchors on the inside of the net at each of the corners. The anchors were made of formed concrete (30.5-cm diameter and 10.2-cm height, constructed by pouring mixed concrete into a form tube) with 2.4-m (5.1-cm diameter) poly-vinyl-chloride (pvc) pipes attached to the center of the anchor to support the block net at each corner. Depletion removal sampling was conducted with a minimum of three and maximum of seven seine passes using a 21.3-m wide, 1.8-m deep, 3.17-mm delta mesh bag seine with a 1.8 x 1.8-m center bag. During each sample pass, one crew member disturbed the shoreline, course woody debris habitat, submersed vegetation and any overhanging tree limbs to displace fish and chase them towards the seine while two other crew members swept the entire site with the net. Subsampling occurred when the number of fish captured was too large to count all individuals per species, or the amount of detritus, filamentous algae, and other vegetation was too great to sort fish in a timely manner. In these cases, I recorded the total sample weight and weighed a subsample (generally 1/10th to 1/20th the total sample) to take back to the lab for processing. The number of fish in the subsample was corrected by the proportion of sample measured to estimate the total number of fish captured per pass.

To estimate the capture probability and absolute density (number of individuals per 1 m^2 site area) of decapods and select small-bodied fishes, I utilized data from a companion State Wildlife Grant project (Camp et al. 2010) where throw trap removal sampling was carried out monthly in the Chassahowitzka River between June 2008 and May 2009, and quarterly between June 2009 and March 2010. During the study, throw trap sampling also occurred monthly in the Homosassa River during November 2008 through December 2009, and quarterly during January 2010 through March 2010. An aluminum throw trap that measured 1 m in width by 1 m in length by 0.75 m in depth was used to sample five habitat types in each study reach, when available, with up to three replicate patches sampled per habitat type. Habitat types included bare substrate, filamentous algae, *Vallisneria americana*, *Potamogeton pectinatus*, and mixed macrophyte/algae patches. The reaches directly above the salt marsh estuary were not sampled with throw traps. Throw trap depletion sampling methods are described in detail by Camp et al. (2011).

The catchability of 12 commonly captured taxa per gear type was estimated from catch and effort information and estimates of absolute density. For fish species within the same genus, *q* was estimated for the genus as a whole. For invertebrates within the same family, *q* was estimated for the family as a whole.

Capture-Recapture Electrofishing Analysis

The following model assumptions were inherent in my analysis of population density and catchability from capture-recapture electrofishing:

- Study reaches were closed to migration, births and deaths over the three-day sample periods,
- all tagged animals were recorded upon recapture,
- capture probability was homogeneous between marked and unmarked animals, and
- catch per unit effort was directly proportional to population density.

Electrofishing relative abundance indices were calculated as the number of fish captured on the first pass divided by the sampling effort measured as electrofishing pedal time in hours. Population abundance was estimated from the Lincoln-Petersen equation (Table 2-1, Equation 1) when at least one marked individual was recaptured during a sampling event. Population density was estimated by dividing the estimated abundance by the area of the study reach (Table 2-1, Equation 2). Reach area was estimated by overlaying polygons onto aerial orthophotographs using ArcGIS® software. Density estimates were scaled to fish per km^2. Electrofishing *q* was estimated from empirically derived data as the ratio of the relative abundance to the estimated population density (Table 2-1, Equation 4).

Seine and Throw Trap Removal Sampling Analysis

The following model assumptions were inherent in my analysis of capture probability and population density from seine and throw trap removal sampling:

- Sites were closed to migration, births and deaths during removal sampling,
- capture probability was constant across sample passes, and
- subsampling of captured fishes provided an accurate sample of the species composition and total catch.

For seines and throw trap removal samples, the abundance and *p* at each site was estimated by multinomial maximum likelihood estimation (Gould and Pollock 1997; Table 2-1, Equation 10). For these two gear types, *q* and *p* estimates were the same, since the sampling intensity (sampling effort divided by area sampled) was equal to 1 when the effort from one pass of sampling was equivalent to the area of the blocked site (Ellis and Wang 2007; Table 2-1, Equation 8). Population density was estimated by dividing the estimated abundance by the site area (200 m^2 for seine samples, and 1 m^2 for throw trap samples).

Distributions of Gear Catchability Estimates

To model the distribution of *q* estimates across taxa, study reaches and sampling events, I calculated the observed frequencies of positive *q* estimates for each gear type and fit the beta probability density function (beta distribution) to the observed frequencies by maximum likelihood estimation. After solving for the alpha (α) and beta (β) shape parameters of the beta distribution, I used a Monte Carlo analysis (10,000 iterations of random draws from the beta distribution with solved parameters) to estimate the mode (q, maximum likelihood estimate), mean ($\overline{q}$), standard deviation (σ), and 95th-percentile lower (95% LL) and upper (95% UL) limits of $\overline{q}$ for each gear type. A two-sided Kolmogorov-Smirnov test (KS test, significance level = 0.05) was conducted to examine the goodness-of-fit of the beta distribution to the observed frequency of q estimates.

Tests for Spatial, Temporal and Interspecific Heterogeneity in Catchability

Akaike information criteria (AIC, Akaike 1974) was used to evaluate alternative models of spatial, temporal and interspecific heterogeneity in q for each gear type (Table 2-3), following methodologies in Anderson (2008) for model based inference. Model AIC values were calculated from the number of model parameters and the total negative log-likelihood (sum of negative log-likelihoods of individual samples). An individual electrofishing sample was defined as a recapture event where at least one individual in the population was released in the reach during previous passes over the three-day sampling period. A seine or throw trap depletion site was considered an individual sample. The log-likelihood of electrofishing samples was equal to the natural log of the binomial probability given the number of trials = marks (M), number of successes = recaptures (R) and probability of success = $p = q$E/A (Table 2-1, Equation 9). All samples were included in the total negative log-likelihood, including samples that failed to recapture marked individuals (i.e. R=0). The log-likelihood of a seine or throw trap sample was equal to the multinomial probability at the maximum likelihood estimate of abundance (N) and p given the observed catches on each pass of the depletion (Table 2-1, Equation 10).

The mean catchability ($\bar{q}$) of individual taxa was estimated by maximum likelihood analysis to compare among populations. I estimated the $\bar{q}$ of individual taxa by solving for the maximum likelihood estimate of the total binomial log-likelihood across all electrofishing recapture events, and total multinomial log-likelihood of seine and throw trap removal sites (i.e. q was allowed to vary by taxa, but was set equal across study reaches and sampling events for a taxa). I calculated the profile-likelihoods (Hilborn and Mangel 1997) to obtain 95% lower (95% LL) and upper (95% UL) credible intervals of $\bar{q}$ for each taxon per gear type.

Estimation of Mean Population Densities of Fishes and Invertebrates

Relative abundance indices were calculated for each taxon per gear type, river, study reach and sampling event as the number of captures divided by sampling effort in hours (electrofishing) or area (seine and throw trap). The mean and standard deviation of relative abundance indices were calculated for each river across all sampling periods. The $\bar{q}$ estimates and credible intervals for each taxon were used to estimate absolute densities and 95% upper and lower limits from mean relative abundance estimates. The absolute density estimates were graphed with relative abundance indices for visual comparison.

Results

Electrofishing Catchability

A total of 354 electrofishing recapture events were conducted on individual populations within the six study reaches (three reaches per river, Figure 2-1), and 126 estimates of electrofishing q were obtained (228 recapture events failed to recapture marked individuals which resulted in estimates of $q = 0$). A histogram of the observed distribution of positive electrofishing q estimates (n = 126) across all taxa, rivers, reaches, seasons and years is presented in Figure 2-2. Maximum likelihood fitting of the beta distribution to the observed positive *q* estimates resulted in beta distribution parameters of $\alpha = 1.15$ and $\beta = 209$ (KS test p-value = 0.015). The maximum likelihood estimate of electrofishing $q = 0.0007$, electrofishing $\bar{q} = 0.0055$ ($\sigma = 0.0052$), 95% LL = 0.0002, and 95% UL = 0.0192.

I utilized all electrofishing capture-recapture data (n = 354) to compare alternative models of heterogeneity in electrofishing *q* (i.e. alternative models allowed for constant *q*, and *q* to vary by river, reach, season, event and taxa). The number of parameters (K), total log-likelihood values (*LL*) from the binomial likelihood, calculated information criteria (AIC_c), and model probabilities (w_i) for each model are listed in Table 2-3. The highest weighted model allowed electrofishing *q* to vary by taxa, and alternative models contained negligible probability in comparison (Table 2-2). Electrofishing $\bar{q}$ for individual taxa (Table 2-3) ranged from 0.0003 (95% LL = 0.0001, 95% UL = 0.0006) for *L. rhomboides* to 0.0160 (95% LL = 0.0070, 95% UL = 0.0291) for *S. ocellatus*. In general, $\bar{q}$ increased for larger-bodied fishes in comparison to smaller-bodied species, with smaller taxa (< 200 mm TL) $\bar{q}$ ranging from 0.0003 (*L. rhomboides*) to 0.0014 (*L. griseus*), and larger taxa (> 200 mm TL) $\bar{q}$ ranging from 0.0017 (*E. sucetta*) to 0.0160 (*S. ocellatus*).

Seine Catchability

I conducted 494 seine removals of individual populations within depletion sites, and obtained 307 estimates of seine *q* (I failed to obtain valid depletions in 53 removals, and excluded estimates from 124 removals that captured fewer than 5 total individuals to avoid low sample bias). A histogram of the observed distribution of *q* estimates (n = 307) across taxa, rivers, reaches, seasons and years is presented in Figure 2-2.

Maximum likelihood fitting of the beta distribution to the observed seine q estimates resulted in beta distribution parameters of $\alpha = 3.41$ and $\beta = 2.10$ (KS test p-value = 0.095). The maximum likelihood estimate of seine $q = 0.686$, seine $\bar{q} = 0.619$ ($\sigma = 0.192$), 95% LL = 0.225, and 95% UL = 0.933.

Seine capture information from all removal samples (n = 494) was used to compare alternative models of heterogeneity in seine q (i.e. alternative models allowed for constant q, and q to vary by river, reach, season, event and taxa). The number of parameters, total log-likelihood values from the multinomial likelihood, calculated information criteria, and model probabilities for each model are listed in Table 2-2. The highest weighted model allowed seine q to vary by taxa, and alternative models contained negligible probability in comparison (Table 2-2). Seine $\bar{q}$ for individual taxa (Table 2-3) ranged from 0.214 (95% LL = 0.185, 95% UL = 0.239) for *G. bosc/M. gulosus* to 0.873 (95% LL = 0.869, 95% UL = 0.878) for *M. beryllina*. In general, I observed the lowest seine $\bar{q}$ for demersal taxa, ranging from 0.214 (*G. bosc/M. gulosus*) to 0.488 (*T. maculatus*), and I measured the highest seine $\bar{q}$ for taxa that were typically captured near the surface of the water column, ranging from 0.739 (*E. harengulus*) to 0.873 (*M. beryllina*). Estimated seine $\bar{q}$ ranged from 0.261 (*S. scovelli*) to 0.739 (*Fundulus* spp.) for taxa associated with vegetation and other structural habitats, including seawalls and woody debris.

Throw Trap Catchability

A total of 1,957 throw trap removals of individual populations were conducted within depletion sites, and 767 estimates of throw trap q were obtained (152 removals failed to obtain valid depletions, and I excluded estimates from 1,038 removals that captured less than 5 total individuals to avoid low sample bias). A histogram of the observed distribution of *q* estimates (n = 767) across taxa, rivers, reaches, seasons and years is presented in Figure 2-2. Maximum likelihood fitting of the beta distribution to the observed throw trap *q* estimates resulted in beta distribution parameters of α = 2.94 and β = 1.23 (KS test p-value = 0.251). The maximum likelihood estimate of throw trap *q* = 0.894, throw trap $\bar{q}$ = 0.706 (σ = 0.200), 95% LL = 0.245, and 95% UL = 0.992.

Capture information from all removal samples (n = 1,957) was used to compare alternative models of heterogeneity in throw trap *q* (i.e. alternative models allowed for constant *q*, and *q* to vary by river, reach, season, event and taxa). The number of parameters, estimated total log-likelihood values of the multinomial likelihood, calculated information criteria, and model probabilities for each model are listed in Table 2-2. Similar to electrofishing and seining, the highest weighted model allowed throw trap *q* to vary by taxa, and alternative models contained negligible probability in comparison (Table 2-2). Throw trap $\bar{q}$ for individual taxa (Table 2-3) ranged from 0.225 (95% LL = 0.186, 95% UL = 0.263) for Grapsidae/Xanthidae (marsh or mud crabs) to 0.950 (95% LL = 0.944, 95% UL = 0.957) for *Palaemonetes* spp. I observed the lowest throw trap $\bar{q}$ for demersal organisms, ranging from 0.225 for Grapsidae to 0.564 (95% LL = 0.528, 95% UL = 0.599) for *G. bosc/M. gulosus*. I estimated relatively high throw trap $\bar{q}$ for organisms that were typically captured near the surface of the water column (*E. harengulus* throw trap $\bar{q}$ = 0.621, *M. beryllina* throw trap $\bar{q}$ = 0.926), as well as for taxa associated with vegetative habitats ($\bar{q}$ ranged from 0.675 for *Lepomis* spp. to 0.950 for *Palaemonetes* spp.).

Relative Abundances versus Absolute Densities

Means and standard deviations of relative abundance indices were compared with absolute density estimates for each taxon per gear type and river (Figure 2-3). The estimated composition of fishes and invertebrates varied between relative abundance indices compared to absolute density estimates. For example, I measured the highest electrofishing relative abundance for *L. griseus* in both rivers; however, absolute density estimates indicated that *E. harengulus* was approximately twice as abundant as *L. griseus*. Similarly, seine relative abundance indices indicated similar catch rates of *Lucania* spp. and *M. beryllina*; however, absolute density estimates demonstrated that *Lucania* spp. were more abundant than all other small-bodied fishes in both rivers. Thus, my results showed that accounting for catchability substantially influenced fish abundance estimates relative to using relative abundance indices.

Discussion

The application of sampling effort in relation to the behavior and spatial distribution of individuals affects the *q* of populations (Winters and Wheeler 1985, Angelsen and Olsen 1987, Swain and Sinclair 1994, Ellis and Wang 2007). To account for variable sampling effort and study area in the assessment of gear efficiency, I calculated relative abundance indices from catch and effort information, scaled absolute abundance estimates by the study area to estimate absolute density, and estimated *q* as the ratio of relative abundance to absolute density. This assessment framework allowed me to appropriately evaluate interspecific, spatial and temporal heterogeneity in gear catchability across study systems and sampling events. My results indicated heterogeneity in *q* estimates between taxa for all gears, and I attributed some of this heterogeneity to habitat use patterns of individual taxa. Other researchers may find the individual taxa $\bar{q}$ estimates and the overall beta distributions of *q* useful as priors for estimating population density and community composition within a broad suite of freshwater and marine ecosystems.

A key finding from this study is that *q* estimates based on population densities are not widely available in the literature, yet are essential for comparison of gear capture probability across space and time. Estimates of *q* and *p* have been published for a multitude of species and study systems (e.g., Mann and Penczak 1984, Bayley and Austen 2002); however, estimates are not directly comparable when the reported values are not scaled by sampling intensity (i.e. the amount of effort applied to a study area). Bayley and Austen (2002) reported experimental estimates of electrofishing *p* for multiple species based on taxa size and environmental covariates, including water depth and macrophyte cover. Using their logistic model and empirical estimates of average fish size, reach depth, and vegetative cover, I predicted electrofishing *q* estimates of *M. salmoides* to be 0.0013 in the Chassahowitzka River and 0.0035 in the Homosassa River (predicted *p* was scaled by mean sampling effort and study area to estimate the predicted *q*). Surprisingly, the predicted values were similar to my observed $\bar{q}$ estimates for *M. salmoides* of 0.0017 in the Chassahowitzka River and 0.0043 in the Homosassa River. Predicted *q* values from Bayley and Austen's (2002) model for *Lepomis macrochirus* were 0.0002 and 0.0011 for the Chassahowitzka and Homosassa rivers, respectively, and my observed values for *Lepomis* spp. were 0.0008 and 0.0043. Discrepancies in the predicted and observed values for *Lepomis* spp. could be due to the fact that the majority of my *q* estimates were for *Lepomis punctatus*, with relatively few estimates for *Lepomis macrochirus*. Studies that report *q* and *p* estimates with undefined sampling intensity are not comparable to other study systems. For example, sampling of a population that is distributed over a relatively small area is not expected to produce an equivalent *p* as the same amount of sampling effort distributed over a much larger area. To account for differences in spatial and temporally heterogeneity in sampling, I recommend estimating *q* for populations based on density estimates, and predicting *p* from the estimated taxa *q* and a defined amount of effort applied to a study area.

Potential biases in my electrofishing *q* estimates may have resulted from violation of the closed capture-recapture model assumptions, tagging mortality, tag loss, or other sources. I examined closure of the study reaches over the three day sampling periods for *M. salmoides* from a concurrent acoustic telemetry study (Pine and Tetzlaff 2008), and concluded that estimates for *M. salmoides* were not likely to be biased as a result of emigration. Other taxa (e.g., *M. cephalus*) are highly mobile and movement out of the study reaches between daily sampling events would result in a negative bias in *q* estimates. Another potential source of bias in electrofishing *q* estimates is tagging mortality. I assessed sampling and tagging mortality for three taxa (*M. salmoides*, *Lepomis* spp. and *E. sucetta*) prior to sampling, and determined that tagging mortality was minimal (0 of 20 *M. salmoides*, 1 of 20 *Lepomis punctatus*, and 0 of 20 *E. sucetta* held in pens died over a three-day observation period), although a negative bias in estimates is possible as a result of sampling mortality or increased susceptibility to predation of tagged animals. Tag loss was not a source of bias, since all tagged individuals were double marked by clipping the left pelvic fin; I was able to detect all tagged individuals when recaptured. Seine and throw trap estimates were not considered biased as a result of migration, due to closure of each site prior to sampling. The density estimates of small-bodied fishes, however, may be biased low as a result of chasing fish away from the site while setting the block net. Behavioral responses of organisms during removal sampling may also result in biased estimates (Peterson et al. 2004). The crew attempted to alleviate the behavioral response bias by scaring fish from structured habitats during each sample pass; however, I was not able to verify that behavioral responses during removal sampling did not negatively bias density estimates of small-bodied fishes and decapods.

Information on *q* of organisms is paramount to researchers whose aim is to accurately assess the composition of aquatic communities. Failure to account for heterogeneity in *q* and *p* can lead to erroneous assessment of trends in population and community metrics when *q* varies spatially, temporally and between taxa; or when changes in effort and area affect the *p* of populations. To estimate the *q* and *p* of populations, I recommend the sampling approach detailed by Pollock et al. (2002) of coupling survey indices with absolute density estimates. This can be accomplished by incorporating capture-recapture, removal or other abundance estimation methods into monitoring program design. For long-term population monitoring, I recommend that researchers estimate *q* during the initial sampling event to examine interspecific and spatial heterogeneity, and periodically throughout the study to evaluate temporal heterogeneity. Large-scale programs may require more advanced tagging methods, such as acoustic or satellite tags, to create a known population of individuals from which *q* can be estimated.

When the relative values of *q* are known, population indices from multiple gears can be appropriately scaled to estimate absolute densities and community composition. My density estimates from electrofishing, seining and throw trapping demonstrate the usefulness of combining density estimates from multiple gears that target different guilds within the community to provide more accurate estimates of community composition compared to sample indices from individual gears. Increased information about the *q* of populations could lead to a greater ability to assess population trends and communities as a whole, particularly in systems that are frequently sampled with more than one gear, such as multispecies fisheries. For these and other multiple-use resources, I advocate that researchers assess *q* for each sampling gear to assess the effectiveness of monitoring in detecting spatial and temporal differences in the structure of communities.

Accurate assessment of community structure provides insight into the complex trophic dynamics that structure population- and community-level processes within aquatic ecosystems (e.g., Kitchell and Crowder 1986, Polis and Strong 1996). Community assessment is a principal component of ecosystem models which provide a centralized framework for linking biotic and abiotic factors to species' population abundance, distribution and dynamics (Hall et al. 1992, Link et al. 2002). These models can elucidate dominant interactions associated with common species, including predator-prey cycles and whole community shifts (Walters and Martell 2004). Community assessment is therefore a critical step in linking population metrics to ecosystem processes.

As natural resource management moves towards integrated ecosystems approaches, the information needs for population and community-level assessments increase greatly. Efficient and broadly-applicable sampling approaches that produce timely and accurate estimates of community composition, density and biomass are greatly needed. Incorporating catchability estimation into large-scale monitoring programs provides the framework needed to efficiently assess community composition from monitoring indices. Such as approach could lead to a greater understanding of community-level dynamics that influence populations, and provide more accurate information to natural resource management programs which regulate populations of organisms and their habitats.

Table 2-1. List of equations used to estimate catchability and capture probability from closed mark-recapture and removal sampling.

Parameter	Equation	Definition of terms	
Population abundance (N):	$N = \frac{C \times M}{R}$	C = total captures during a sample pass M = number of marked fish within a study reach R = number of recaptures	(1)
Population density (D):	$D = \frac{N}{A}$	A = area of the study reach (kilometers^2)	(2)
Catchability equation:	$\frac{C}{E} = q \times D$	E = effort applied during a sample pass (hours)	(3)
Catchability coefficient (q):	$q = \frac{C}{E \times D}$		(4)
	$q = \frac{R \times A}{M \times E}$		(5)*
Probability of capture (p):	$p = \frac{C}{N}$		(6)
	$p = \frac{R}{M}$		(7)†
	$p = \frac{q \times E}{A}$		(8)‡
Log-Likelihood Equations:			
Capture-recapture binomial log-likelihood equation:	$LL(q \mid M, R, A, E) = LN\left(\frac{M!}{R!(M-R)!}\right) + R \times LN\left(\frac{q \times E}{A}\right) + (M-R) \times LN\left(1 - \frac{q \times E}{A}\right)$		(9)
Removal multinomial log-likelihood equation:	$LL(N, p \mid C_{1 \to k}) = LN\left[\frac{N!}{(\prod_{i=1}^{k} C_i!)(N - \sum_{i=1}^{k} C_i)!}\right] + \sum_{i=1}^{k} \left\{C_i \times LN\left[p(1-p)^{i-1}\right]\right\} + \left(N - \sum_{i=1}^{k} C_i\right) \times LN\left[(1-p)^k\right]$		(10)§

*Substitution of Equation 1 into Equation 2, and Equation 2 into Equation 4 solves to Equation 5. †Substitution of Equation 1 into Equation 6 solves to Equation 7. ‡Substitution of Equation 7 into Equation 5 solves to Equation 9. §k is the number of passes in the depletion sample, q = p when effort is equal to the site area.

Table 2-2. Akaike information criteria and model probabilities (w_i) for alternative models of spatial, temporal and interspecific heterogeneity in catchability of fishes and invertebrates sampled by electrofishing, seining and throw trapping.

Gear	n	Model	K	*LL*	Δ AIC_c	w_i
Electrofishing	364	q(constant)	1	-502	198	0.0
		q(river)	2	-427	50	0.0
		q(reach)	6	-415	35	0.0
		q(season)	2	-498	192	0.0
		q(event)	4	-494	188	0.0
		q(taxa)	12	-391	0	1.0
Seine	494	q(constant)	1	-34,501	22,101	0.0
		q(river)	2	-33,610	20,320	0.0
		q(reach)	6	-23,573	255	0.0
		q(season)	2	-34,381	21,862	0.0
		q(event)	4	-30,740	14,585	0.0
		q(taxa)	12	-23,439	0	1.0
Throw trap	1,957	q(constant)	1	-9,938	4,533	0.0
		q(river)	2	-9,609	3,877	0.0
		q(reach)	4	-9,254	3,171	0.0
		q(season)	4	-9,908	4,478	0.0
		q(event)	20	-9,545	3,786	0.0
		q(taxa)	12	-7,661	0	1.0

Table 2-3. Number of estimates (n), mean catchability ($\bar{q}$), and 95th percentile lower and upper limits of mean catchability for individual taxa sampled by electrofishing, seining and throw trapping.

	n	$\bar{q}$	95%LL	95%UL
Electrofishing				
Ameiurus spp.	12	0.0038	0.0005	0.0114
Archosargus probatocephalus	23	0.0090	0.0043	0.0160
Centropomus undecimalis	28	0.0058	0.0032	0.0094
Erimyzon sucetta	16	0.0017	0.0010	0.0027
Eucinostomus harengulus	35	0.0004	0.0003	0.0007
Lagodon rhomboides	34	0.0003	0.0001	0.0006
Lepisosteus platyrhincus	25	0.0078	0.0049	0.0115
Lepomis spp.	41	0.0011	0.0009	0.0014
Lutjanus griseus	42	0.0014	0.0012	0.0016
Micropterus salmoides	47	0.0023	0.0019	0.0028
Mugil cephalus	43	0.0020	0.0012	0.0031
Sciaenops ocellatus	18	0.0160	0.0070	0.0291
Seine				
Callinectes sapidus	45	0.365	0.296	0.428
Eucinostomus harengulus	66	0.739	0.732	0.746
Fundulus spp.	15	0.739	0.659	0.805
Gobiosoma bosc/Microgobius gulosus	61	0.214	0.185	0.239
Lagodon rhomboides	47	0.406	0.378	0.433
Lepomis spp.	33	0.497	0.468	0.524
Lucania spp.	65	0.409	0.404	0.413
Menidia beryllina	41	0.873	0.869	0.878
Notropis spp.	17	0.462	0.443	0.481
Strongylura spp.	36	0.774	0.741	0.806
Syngnathus scovelli	36	0.261	0.192	0.323
Trinectes maculatus	32	0.488	0.423	0.545
Throw Trap				
Callinectes sapidus	128	0.592	0.535	0.646
Cambaridae	191	0.522	0.494	0.55
Eucinostomus harengulus	73	0.621	0.579	0.662
Gobiosoma bosc/Microgobius gulosus	195	0.564	0.528	0.599
Grapsidae	163	0.225	0.186	0.263
Lagodon rhomboides	41	0.770	0.654	0.862
Lepomis spp.	198	0.675	0.654	0.695
Lucania spp.	388	0.827	0.822	0.833
Menidia beryllina	91	0.926	0.909	0.941
Notropis spp.	45	0.961	0.931	0.981
Palaemonetes spp.	224	0.950	0.944	0.957
Syngnathus scovelli	220	0.684	0.651	0.716

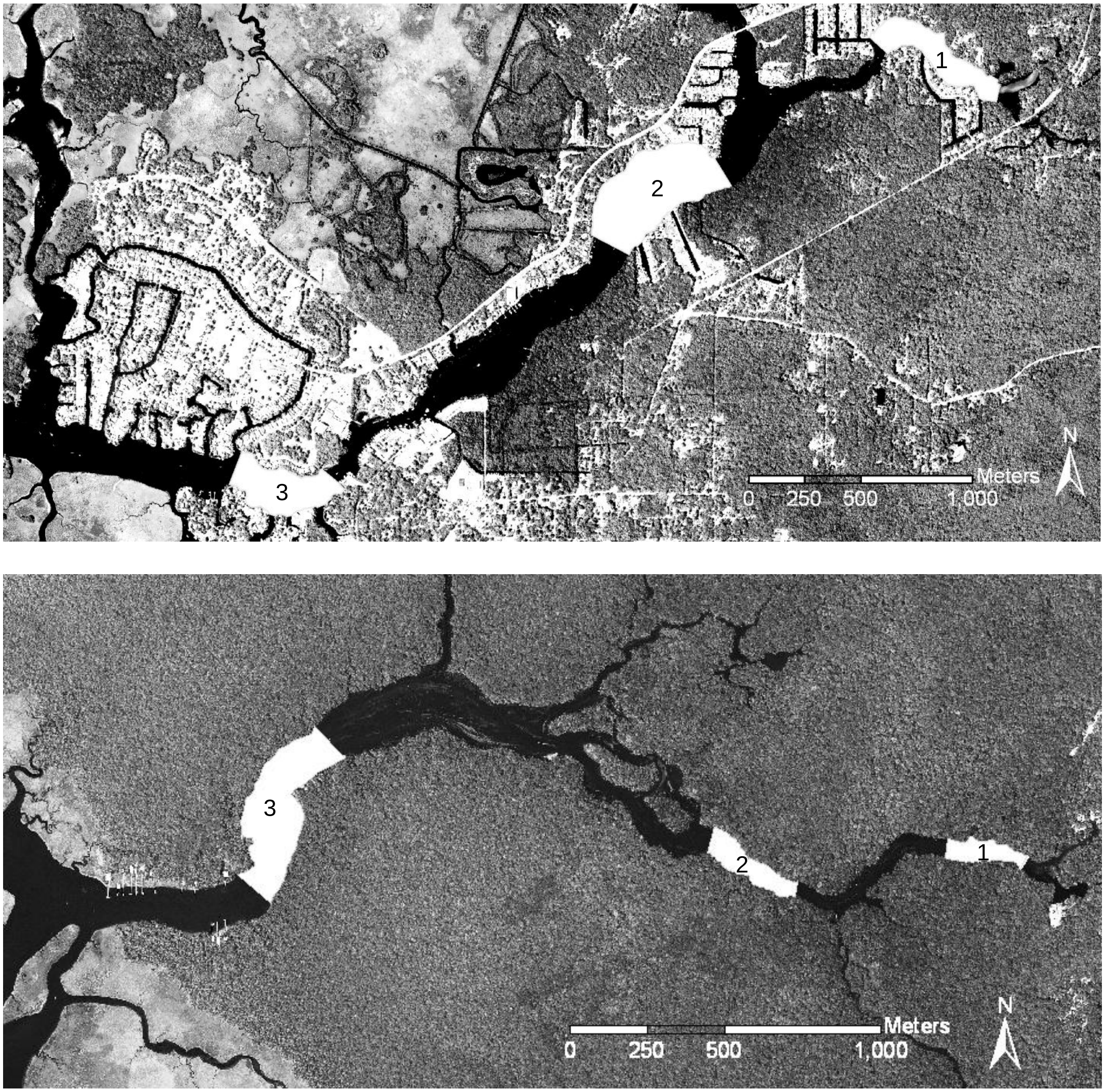

Figure 2-1. Study reaches within the Homosassa and Chassahowitzka rivers, Florida.

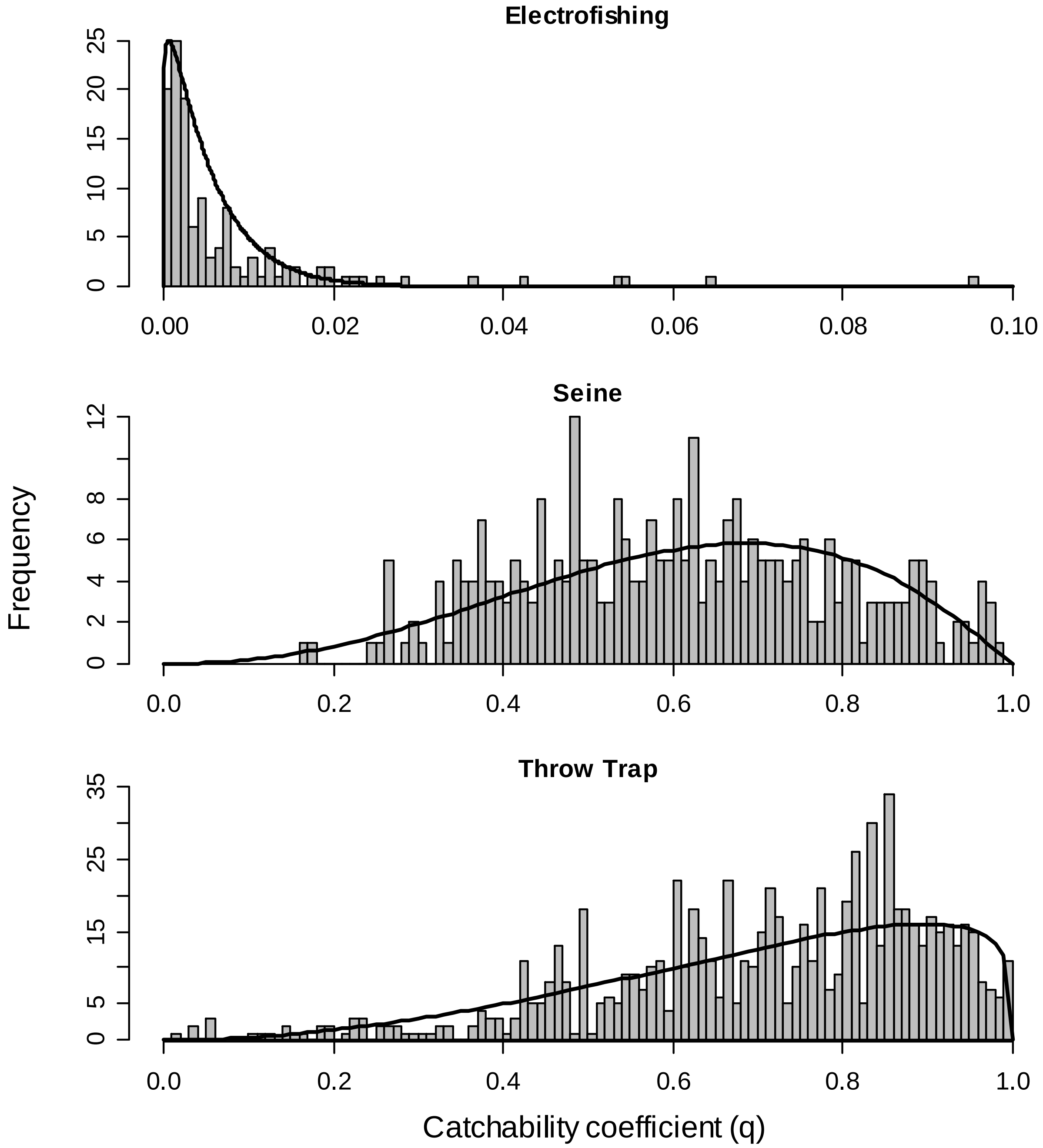

Figure 2-2. Histograms of observed positive catchability estimates (q) across all taxa measured. Non-linear curves represent the fitted beta distributions. Note the difference in scale of the x-axis between electrofishing and the other two gears as a result of the scaling by units of effort.

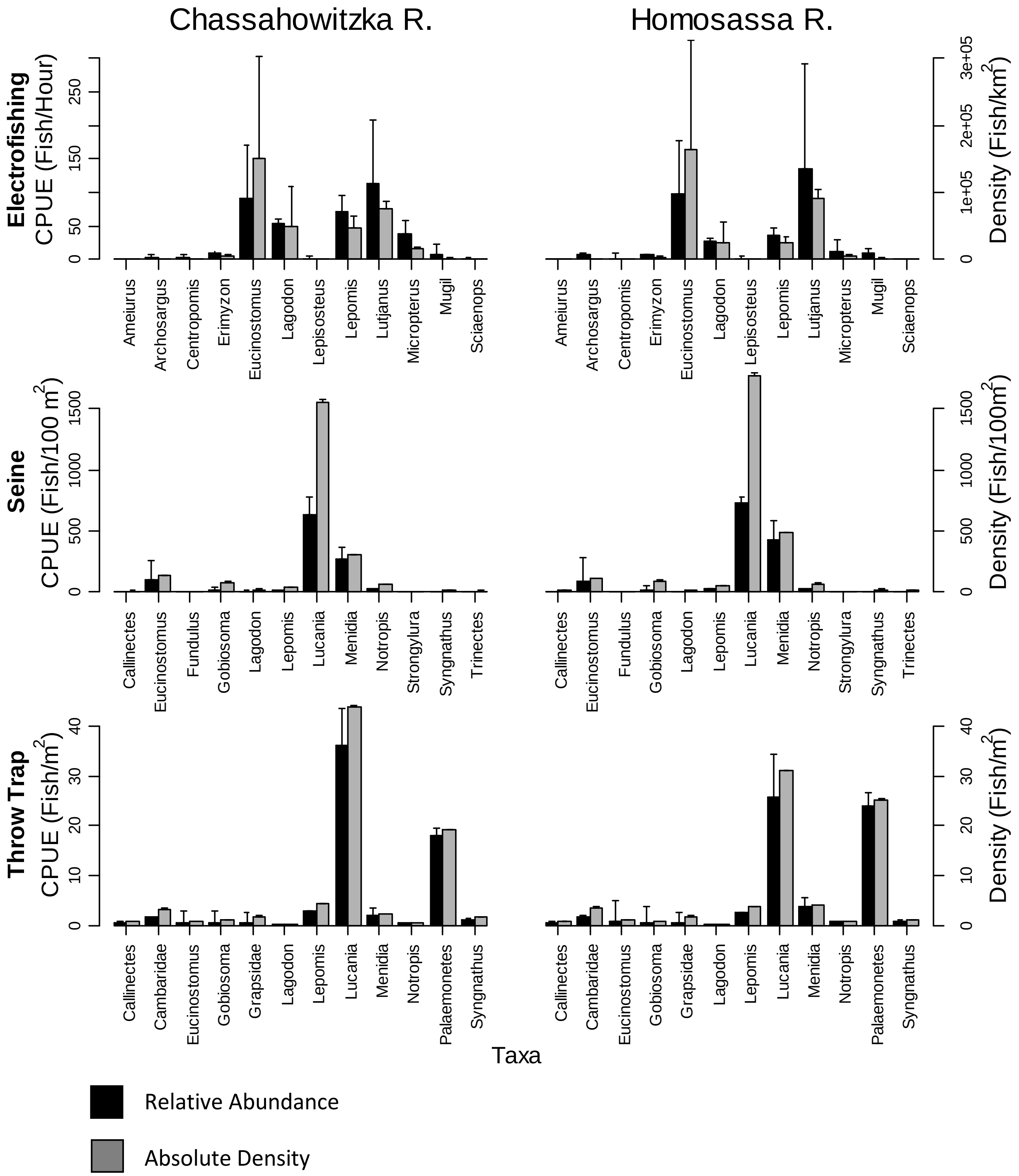

Figure 2-3. Relative abundance indices (CPUE = catch per unit effort) and absolute density estimates of taxa commonly detected during boat electrofishing, seine and throw trap sampling within the Chassahowitzka and Homosassa rivers.

CHAPTER 3
THE COMPOSITION AND BIOMASS OF THE AQUATIC COMMUNITIES WITHIN THE CHASSAHOWITZKA AND HOMOSASSA RIVERS

Introduction

Ecosystem-based approaches to natural resource management and restoration are widely recommended (Grumbine 1994, Lindenmayer et al. 2000, Pew Oceans Commission 2003, Pikitch et al. 2004, Ocean Studies Board 2006) and increasingly required (e.g., Magnuson-Stevens Fisheries Conservation and Management Act Section 406, Malone 1995). Mandates for ecosystem research are motivated by explicit recognition of the roles of predation (Menge and Sutherland 1976, Bowlby and Roff 1986, Estes et al. 1998), competition (MacArthur 1958, Connell 1961, Schoener 1983), trophic dynamics (Hairston et al. 1960, Paine 1980, Carpenter et al. 1985), and environmental conditions (Sandoey and Nilssen 1987, Ritchie 2000) in structuring populations. This recognition has emphasized the need to link assessments of individual species with broader-scale community and ecosystem studies (Link 2002, Pikitch et al. 2004, Walters et al. 2005). Ecosystem research, including the quantitative assessment of community structure and the function of ecosystem components, is central to the development of effective management and restoration programs for renewable natural resources.

The assessment of community structure is a central component of ecosystem studies (Karr 1987), and is essential for the development of food-web models aimed at evaluating management policy options and predicting ecosystem effects of environmental changes (Christensen and Pauly 1992). At a minimum, a quantitative characterization of community structure requires concurrent sampling of populations from multiple trophic levels to estimate the composition of producers, primary consumers, and predators; and an examination of trophic interactions among key taxa. Information on community structure provides insight into the complex trophic dynamics that influence a broad suite of population- and community-level processes within aquatic ecosystems (Polis and Strong 1996, Kitchell and Crowder 1986, Levin and Paine 1974). Furthermore, community assessment is a principal component of ecosystem models which provide a centralized framework for linking biotic and abiotic factors to species' population abundance, distribution and dynamics (Hall et al. 1992, Link et al. 2002). These models can elucidate dominant interactions that occur among common species, including predator-prey relationships and whole community shifts (Walters and Martell 2004). Community assessment is therefore a critical step in linking population metrics to ecosystem processes, such as habitat loss.

The experimental removal of key habitat components has been shown to alter the community structure of fishes within aquatic ecosystems (Bettoli et al. 1993, Deegan et al. 2002, Sass et al. 2006). Bettoli et al. (1993) demonstrated a shift in fish community structure associated with the large-scale removal of aquatic vegetation resulting from the stocking of grass carp in Lake Conroe, Texas, including the decline or collapse of small phytophilic populations. Sass et al. (2006) showed that the removal of course woody debris from the littoral zone of lakes in Wisconsin altered growth, predation and recruitment of fish populations. These ecosystem manipulations demonstrated how removal of critical habitats affected fish populations disparately, leading to a shift in species assemblages and community dynamics. In general, habitat loss is expected to alter the community structure within aquatic ecosystems; however, the effects of macrophyte loss on stream faunal communities have not been quantitatively assessed.

Since the experimental removal of vegetative habitat is not always a viable option for assessing community effects of habitat loss, a comparative analysis of community structure between ecosystems with contrasting vegetative habitats may elucidate key consequences of habitat loss to fish and invertebrate populations.

I quantified the composition and biomass of the aquatic communities within two spring-fed, coastal rivers in Florida to make spatial and temporal comparisons between a highly vegetated river, the Chassahowitzka River, and one where macrophytes have been largely absent for nearly a decade, the Homosassa River. Historically, these systems were reported to be some of the most productive ecosystems in the world (Odum 1957), supporting unique, oligohaline communities comprised of marine and freshwater plants, fishes and invertebrates (Herald and Strickland 1949, Odum 1953). I hypothesized that large-scale habitat loss in the Homosassa River resulted in an altered composition of fishes compared to qualitative observations of the fish community recorded 60 years ago (Herald and Strickland 1949). I also hypothesized that the current fish and invertebrate community compositions in the Homosassa River differs from that of the Chassahowitzka River, which supports greater abundance of macrophytes, including *Vallisneria americana*, *Potamogeton* spp., *Najas guadalupensis*, *Myriophyllum spicatum* (non-native), and *Hydrilla verticillata* (non-native). To test this, I sampled fishes, invertebrates, macrophytes and algae using multiple gears (electrofishing, seines, throw traps, benthic cores, invertebrate nets, and vegetation quadrats), and utilized information on taxa specific gear catchability (Chapter 2), to estimate the absolute density and biomass of select trophic groups and obtain estimates of community composition. I examined the seasonal and spatial composition of the aquatic communities for the purpose of identifying key differences between rivers with disparate vegetative habitat composition and biomass, and qualitatively evaluate changes in the Homosassa River compared to historical observations prior to habitat loss. While community-level assessments are relatively rare, quantitative estimates are necessary for inferring how vegetative habitat loss may affect fish and invertebrate communities in stream ecosystems.

Methods

To assess the composition and biomass of the aquatic communities within the Chassahowitzka and Homosassa rivers, I utilized data from multiple gear types that targeted different guilds of fishes and invertebrates (i.e. benthic invertebrates, plant-associated invertebrates, decapods, small-bodied fishes, and large-bodied fishes). All sampling was conducted in conjunction with the long-term submersed aquatic vegetation (SAV) monitoring program (Frazer et al. 2006). Standardized quadrat sampling methods utilized in the long-term vegetation monitoring program were implemented to estimate the biomass of macrophytes and filamentous algae in each of the study reaches (Figure 2-1). Sediment cores and 300-μm mesh nets were used to collect grab samples of macroinvertebrates associated with benthic habitats and SAV. In addition to sediment cores and vegetation nets, I utilized data collected during a concurrent throw trap sampling program for decapods (Camp et al. 2011), including blue crabs (*Callinectes sapidus*), crayfish (Cambaridae), mud crabs (Grapsidae and Xanthidae) and grass shrimp (*Palaemonetes* spp.). To sample the fish community in the rivers, seine sampling was used to capture small-bodied fishes and electrofishing was used to capture large-bodied fishes. Sampling occurred across multiple spatial (stratified study reaches in each river) and temporal (monthly, seasonally and yearly) scales to more accurately estimate the average biomass of fishes and invertebrates within the rivers, and assess variation in estimates over the period of study.

Submersed Aquatic Vegetation Sampling and Analyses

To estimate the percent cover and biomass of macrophytes and filamentous algae in coastal rivers, I utilized standardized quadrat sampling methods outlined by Frazer et al. (2006) for long-term SAV monitoring. Sampling was conducted biannually in August and February during years one and two of the project, and monthly during year three. I assumed perfect detection ($p = 1$) for plants and algae collected in quadrats. Biomass was estimated as wet weight of plants or algae per quadrat area. I calculated the mean and standard deviation of macrophyte and filamentous algae biomass for each study reach. I scaled all biomass estimates to g per 100 m^2 area.

Invertebrate Sampling and Analyses

I sampled aquatic invertebrates associated with sediments and above-bottom portions of SAV in the three study reaches of both rivers during August and February of year one, and collected invertebrates inhabiting SAV in Reaches 1 and 2 of years two and three. Sampling occurred concurrently with SAV monitoring along three fixed transects within each of the study reaches. I sampled five stations (equally spaced) along each transect. I collected benthic invertebrates with a 5-cm inner-diameter acrylic push-core (sediment surface area sampled = 20 cm^2). To obtain a sample, the core was firmly pushed into the sediments to a depth of 10 cm (volume sampled = 200 cm^3) and then carefully withdrawn. I then extruded the sample from the push-core into a 1-L container or 1-gallon, sealable, labeled plastic bag and rinsed any sample portions remaining inside the push-core into the sample container.

To estimate the density and biomass of macroinvertebrates associated with SAV, I sampled 15 uniformly stratified sites per reach with a 300-μm mesh, netted ring sampler (inner ring diameter = 252 mm, 0.05 m^2 area). I obtained samples by placing the open bottom ring of the sampler over a portion of SAV, closing the bottom of the net, and cutting the SAV just above the sediment/water interface. I rinsed the sample into a 1-L sample container or 1-gallon sealable plastic bag and labeled it with the sample location and date. I placed all samples on ice immediately after collection and transported them to the Florida Fish and Wildlife Conservation Commission, Gainesville Fisheries Research Laboratory or University of Florida, Florida Rivers Research Laboratory for processing and taxonomic identification.

In the laboratory, individual samples were rinsed from containers into a 300-μm mesh sieve to remove water, placed in 1-L, wide-mouth plastic or glass jars and preserved with 95% ethanol (year one) or were frozen (years two and three). During year one, entire samples were processed by placing small portions into a petri dish, covering each portion with water, and inspecting the contents under a stereo-dissecting microscope with magnification to 63x. Invertebrates were removed from petri dishes with forceps, identified to major taxonomic group, enumerated and then preserved in labeled vials with 95% ethanol. A laboratory sheet was prepared listing taxa and counts for each sample. During years two and three, invertebrate samples were white-panned to remove and enumerate visible macroinvertebrates. The SAV sample was then rinsed over the white pan, sieved, weighed, and subsampled (by wet weight). Invertebrates were removed from the SAV subsample and individual taxa were enumerated under a stereo-dissecting microscope. The fine particles and remaining periphyton in the white pan were then sieved, weighed and subsampled (by wet weight). The invertebrates from the fine material subsample were removed with forceps and enumerated by individual taxa under a stereo-dissecting microscope. I corrected invertebrate counts for each subsample by dividing by the proportion of sample measured, and summed the estimate with the counts from the white pan. I assumed perfect detection (p = 1) of invertebrates sampled with benthic cores and vegetation nets. I calculated invertebrate density as the mean number of individuals per taxa per sample divided by the sampled surface area. I calculated the mean density and standard deviation of invertebrates for each study reach and scaled the estimate to 100-m^2 area. Separate analyses were conducted for benthic and SAV substrates. I calculated biomass estimates of selected taxa by multiplying the estimated density by mean individual mass. I obtained dry mass estimates for individual taxa from samples that were sorted, enumerated, weighed and dried, or from published length-mass regressions (Benke et al. 1999) and measurements of mean individual length (total length was measured for amphipods, insects, tanaids, and isopods; and shell length was measured for gastropods). Dry mass estimates were converted to wet mass using conversion factors published by Ricciardi and Bourget (1998).

Blue crabs, mud crabs, crayfish and grass shrimp were not effectively captured by benthic cores or vegetation nets; therefore, I utilized data from Camp et al. (2011) to obtain biomass estimates of these invertebrates. The absolute densities were estimated from throw trap depletion samples taken within the study reaches during the period of study. Absolute densities in each study reach were estimated by the multinomial likelihood approach for depletion sampling described by Gould and Pollock

(1997). The absolute biomasses were estimated by multiplying the estimated density by average mass per individual. Estimates for each study reach were scaled to g per 100-m^2 area and the average biomass in the river was estimated across study reaches (Reaches 1 and 2). The lower study reaches in both rivers were not sampled with throw traps.

Fish Sampling and Analyses

I deployed two gear types (electrofishing and seining) to estimate the abundance and biomass of large- and small-bodied fishes. Three-day mark-recapture electrofishing events and three-day block-net seine depletion sampling occurred during four sample periods (summer 2007, winter 2008, summer 2008, and winter 2009) in each river. Electrofishing occurred biannually during the second and third weeks of July and January of years one and two. During biannual sampling, each study reach was electrofished once per day for three consecutive days. During year three, single-pass electrofishing and seine surveys were conducted monthly. Standardized sample locations are shown for each gear type in Figure 2-1. Electrofishing reaches included four shoreline transects and three mid-stream transects. I defined one shoreline transect as the section of littoral stream bank between long-term SAV monitoring transects and mid-stream transects overlapped the SAV monitoring transects.

During years one and two of the project, I sampled nine multi-pass seine depletion sites biannually (August 2007, February 2007, August 2008, and February 2009) in each river to assess the small-bodied fish community and obtain estimates of gear catchability. I sampled three sites in each reach at fixed locations that coincided with electrofishing, long-term SAV monitoring, and invertebrate sampling transects. Sites ranged in size between 200 and 600 m^2 during the first sampling event, but were standardized at 20 m in length and 10 m in width during subsequent sampling. I chose the location of each seine depletion site within a reach randomly without replacement and assigned one of three possible locations: river right, mid-stream or river left. All three locations were sampled at separate transects within a study reach. A 2.4-m deep block-net was set around each site, and multiple pass sampling (three to seven passes per site were completed until a decline in catches was observed) was executed with a 21.3-m wide, 1.8-m deep, 3.17-mm delta mesh bag seine with a 1.8 x 1.8-m center bag. During year three, monthly single-pass seine surveys were conducted at block-netted sites. At most sites, subsampling occurred when either the number of fish captured was too large to count all individuals per species, or the amount of detritus, filamentous algae, and other vegetation was too great to sort fish in a timely manner. When subsampling occurred, I recorded the total weight of the sample and weighed a portion to take back to the lab for processing. I then corrected the number of fish in the subsample by the proportion of sample measured to estimate the total number of fish captured per pass.

All fish captured were identified to species, when possible, otherwise fish were identified to the lowest possible taxonomic resolution. All fish were measured for total length (TL) and weight (weights were not taken when windy conditions prevented accurate measurement) and released, with the exception of fishes kept for diet and growth analyses. During electrofishing sampling, every fish greater than 150 mm TL was tagged in the dorsal fin pterygiophores with a t-bar external tag containing a unique identification number. The right pelvic fin of every fish greater than 50 mm TL was clipped as a secondary mark for externally-tagged fish and primary batch mark for fish between 50 and 150 mm in TL.

Electrofishing catch per unit effort (CPUE) was calculated for each taxon (i) per sampling event (t) as the number of fish captured (C) within a reach divided by sampling effort (E) in hours:

$$CPUE_{i,t} = \frac{C_{i,t}}{E_t} \tag{3-1}$$

Electrofishing CPUE was averaged across days for multiple-pass sampling during years one and two. Seine and throw trap CPUE were calculated as the number of individuals captured on the first pass of netting divided by area swept (seine unit of effort = 100 m^2; throw trap unit of effort = 1 m^2). Seine and throw trap CPUE were averaged across sites within a reach. Absolute density was estimated for each taxon as mean CPUE divided by mean catchability ($\overline{q}$) (Table 2-3):

$$D_{i,t} = \frac{CPUE_{i,t}}{\overline{q_i}} \tag{3-2}$$

The sampled mean CPUEs were assumed equal to the population means, and confidence intervals of density estimates were estimated from 95% confidence intervals of mean catchability (Table 2-3). The biomass (B) of each taxon was estimated by multiplying the density times the mean weight of individuals (w) captured within the reach:

$$B_{i,t} = D_{i,t} w_{i,t} \tag{3-3}$$

All estimates were scaled to g per 100-m^2 area for comparison between reaches and rivers.

Results

Submersed Aquatic Vegetation (SAV)

Average SAV cover varied between 11 and 52% during August sampling in Reaches 1 and 2 of the Chassahowitzka River, and varied between 47 and 77% during February sampling. I observed minimal SAV cover in Reach 3 of the Chassahowitzka River during August sampling (0 to 2%), but estimated considerable filamentous algae cover during February of each year (21 to 30%). Average filamentous algae cover in Reach 1 of the Homosassa River peaked in August 2007 (29%), and ranged between 7 and 25% during the other sample periods. I documented the highest average percent cover in Reaches 2 and 3 of the Homosassa River during February 2008 and 2009 (27 to 56%).

The estimated biomass of macrophytes was distinctly different between the Chassahowitzka and Homosassa rivers (Figure 3-1), and both systems demonstrated a strong seasonality in filamentous algae biomass (Figure 3-2). SAV within the Chassahowitzka River during August of each year was comprised primarily of macrophytes (mean plant biomass = 782, 1433, and 1728 g/m^2 in 2007, 2008 and 2009, respectively; mean algae biomass = 35, 34, 17 g/m^2 in 2007, 2008 and 2009, respectively). I measured the greatest mean plant biomass in Reach 1 (782 to 1728 g/m^2), with lower biomasses observed in Reaches 2 (140 to 1246 g/m^2) and 3 (0 to 9 g/m^2) (Figure 3-1). The Homosassa River was nearly devoid of macrophytes across all sample periods (0 to 45 g/m^2) (Figure 3-1). I documented seasonally high biomass of filamentous algae during winter (2008 and 2009) and spring (2010) sampling periods in both rivers (Table 3-1, Figure 3-2).

Invertebrates

Nematodes, ostracods, oligochaetes, polychaetes, amphipods, copepods, and chironomids were common in sediment samples collected from both rivers during August 2007 and February 2008. Sediment samples were not processed after the initial two sample periods due to logistical and funding constraints. Benthic invertebrate biomass (measured as the sum of ostracods, oligochaetes, polychaetes, amphipods, nematodes, copepods, and bivalves) averaged 67 g/100 m^2 during August 2007 and 166 g/100 m^2 during February 2008 within the Chassahowitzka River, and 41 g/100 m^2 during August 2007 and 493 g/100 m^2 during February 2008 within the Homosassa River.

The most numerous taxa associated with SAV samples included amphipods, ostracods, gastropods, copepods, isopods, nematodes chironomids and other insect larvae. I estimated higher total biomass of invertebrates associated with SAV (measured as the sum of gastropods, insects, isopods and tanaids) during February sampling periods (mean biomass in the Chassahowitzka River = 578 g/100 m^2, Homosassa River = 5023 g/100 m^2) compared to August (mean biomass in the Chassahowitzka River = 315 g/100m^2, Homosassa River = 103 g/100 m^2) in both rivers. Biomass estimates for vegetation associated invertebrates included samples from all biannual sampling periods; however, I was not able to process monthly invertebrate samples from year three due to logistical and funding constraints. Amphipods were analyzed separately from other vegetation associated invertebrates due to their relatively high biomass in both rivers compared to other taxa (mean August biomass = 189 g/100 m^2 in the Chassahowitzka River and 191 g/100 m^2 in the Homosassa River), large increases in biomass associated with winter sampling (mean February biomass =

2316 g/100 m^2 in the Chassahowitzka River and 1562 g/100 m^2 in the Homosassa River) (Figure 3-3), and importance as prey for fishes (Chapter 4). Vegetative net sampling did not effectively capture larger invertebrate taxa, including blue crab (*Callinectes sapidus*), crayfish (Cambaridae), mud crab (Grapsidae and Xanthidae combined) and grass shrimp (*Palaemonetes* spp.). Density and biomass estimates of these larger invertebrates were obtained from throw trap sampling data collected during a concurrent study (Camp et al. 2011). Mean biomass estimates of each invertebrate taxon by river and season are listed in Table 3-1.

The density and biomass of invertebrates associated with SAV was greatest during winter sampling periods when filamentous algae biomass was high (Figures 3-3 through 3-7). This pattern was apparent for the most abundant taxa of invertebrates with the exception of insects(Figures 3-3 through 3-7). In fact, insect density and biomass was similar across all sampling periods in the Chassahowitzka River, and I observed a relatively high biomass of insects in the Homosassa River during February 2008 when filamentous algae mats were prevalent (Figure 3-4). Insects, particularly chironomids, were abundant in both filamentous algae and macrophyte samples. Of all taxa sampled, amphipods and blue crabs demonstrated the greatest biomass in the Chassahowitzka River, and amphipods and mud crabs were most abundant in the Homosassa, with peak biomass occurring during winter periods (Table 3-1). One surprising result was the observed higher density and biomass of gastropods associated with filamentous algae during winter in the Homosassa River compared to the Chassahowitzka River which supports vegetation year-round (Figure 3-5).

Small-bodied Fishes

Overall, freshwater small-bodied fishes were less abundant in the Homosassa River compared to the Chassahowitzka River (Figure 3-8); however, many saltwater species showed similar biomass between the two rivers with the exception of pinfish (*Lagodon rhomboides*) which occurred in higher biomass within the Chassahowitzka River and gobies (*Gobiosoma bosc*, *Microgobius gulosus*) which occurred in higher biomass in the upper reaches of the Homosassa River. I estimated greater density and biomass of small-bodied fishes in the upper two study reaches of the Chassahowitzka River during August sampling events compared to the Homosassa River (Figures 3-8 and 3-9). Small-bodied fish density and biomass declined between summer and winter sampling in the Chassahowitzka River during all years, which may be attributed, in part, to decreased biomass of freshwater species (Figure 3-8). In contrast, I did not observe a higher density and biomass of small-bodied fishes during summer periods in the Homosassa River.

Many small-bodied species showed a strong seasonality in their density and biomass, with the greatest biomass observed in late spring through summer, and relatively low biomass during fall and winter (Figures 3-8 and 3-9). Seine sampling within the Chassahowitzka River during August primarily captured rainwater killifish (*Lucania parva*), followed by inland silverside (*Menidia beryllina*), tidewater mojarra (*Eucinostomus harengulus*), bluefin killifish (*Lucania goodei*), and young-of-the-year spotted sunfish (*Lepomis punctatus*). February sampling within the Chassahowitzka River predominantly captured rainwater killifish, tidewater mojarra, pinfish, needlefish (*Strongylura* spp.) and gray snapper (*Lutjanus griseus*). Seining within the Homosassa River during August produced mostly rainwater killifish, inland silverside, tidewater mojarra, clown goby (*Microgobius gulosus*) and naked goby (*Gobiosoma bosc*). February sampling in the Homosassa River captured tidewater mojarra, rainwater killifish, mosquitofish (*Gambusia holbrooki*), bay anchovy (*Anchoa mitchilli*), inland silverside, clown goby and naked goby.

Large-bodied Fishes

The estimated biomass of freshwater fishes was significantly greater in the Chassahowitzka River compared to the Homosassa River for most sampling periods (Figures 3-10 through 3-14). Mean biomass estimates of large-bodied fishes are listed by species or trophic group in Table 3-1. Total freshwater and saltwater large-bodied fish biomass was greatest in Reach 1 of both rivers with lower biomass observed in downstream reaches. I estimated significantly lower biomass of lake chubsucker (Figure 3-10), *Lepomis* spp. (Figure 3-11), and adult largemouth bass (Figure 3-14) in the Homosassa River relative to the Chassahowitzka River during most sampling events; however, Florida gar (*Lepisosteus platyrhincus*) were more abundant in the Homosassa River (Figure 3-13) and comprised a large proportion of the freshwater, large-bodied fish biomass. I measured a large increase in the biomass of lake chubsucker (Figure 3-10) and *Lepomis* spp. (Figure 3-11) between January 2008 and July 2009 within the Chassahowitzka River, corresponding with relatively strong cohorts of young-of-the-year captured during summer 2008 and subsequent sampling events. I documented high densities and biomass of saltwater, large-bodied fishes during winter sampling periods of each year in both rivers (Figures 3-15 through 3-20), with the greatest biomass surveyed during January 2008 within Reach 1 of the Homosassa River.

Common fishes captured by electrofishing during August in both rivers included pinfish, spotted sunfish, largemouth bass, striped mullet (*Mugil cephalus*) and American eel (*Anguilla rostrata*). Lake chubsucker were also commonly captured in the Chassahowitzka River, but were rarely encountered in the Homosassa River (5 total young-of-the-year were captured during the period of study). Gray snapper were the most abundant species captured during January within both rivers, followed by spotted sunfish, pinfish, largemouth bass and lake chubsucker within the Chassahowitzka River; and striped mullet, spotted sunfish and common snook (*Centropomus undecimalis*) within the Homosassa River. A complete list of scientific and common names of freshwater and saltwater fish species captured during electrofishing and seine sampling within each river is provided in Tables 3-2, 3-3, 3-4 and 3-5. The spatial and temporal variability in biomass estimates is illustrated in Figures 3-10 through 3-20.

Discussion

The Chassahowitzka River supported greater vegetative habitat cover and biomass year-round in the upper reaches compared to the Homosassa River as a result of the perennial cover and biomass of macrophytes. Filamentous algae were prevalent in both systems during winter sampling periods, creating a seasonally abundant habitat for invertebrates and small-bodied fishes, such as amphipods, isopods, gastropods, and killifish. Vegetative habitat was low in abundance during the rest of the year in the Homosassa River. In areas with higher flows, algae mats were transported to downstream reaches where they senesced in areas with lower velocity and higher salinities (Frazer et al. 2006). This may have resulted in displacement of organisms utilizing the vegetative habitat in the Homosassa River to alternative habitats such as littoral areas or benthic substrates, whereas invertebrates and fishes in the Chassahowitzka River may use alternative, perennial vegetative habitats.

I documented relatively large declines in freshwater species density and biomass during winter sampling periods, coincident with immigration of saltwater species that utilize these systems, likely as thermal refugia, including gray snapper, common snook and red drum. Declines in large-bodied freshwater species density during winter periods are due, in part, to migration into tributaries, canals and headwater areas, as evidenced by resighting observations of marked fish outside of the study reaches during subsequent months after sampling (Frazer, unpublished data). The sharp decline in small-bodied fishes during winter may be a result of increased predation by saltwater piscivores or migration out of the study area, which, in turn, may release predation pressure on small invertebrates and increase the density and biomass of taxa that are exploited as prey by small-bodied fishes. Additionally, filamentous algae mats may provide temporary refuge for small invertebrates allowing populations densities to increase under lower predation pressure; however, mortality estimates of invertebrates were not conducted as part of this study. Overall, I observed similar patterns in fish density and biomass as those observed for estimated biomass of SAV in the study systems (i.e. reaches and sampling periods with higher biomass of SAV, including macrophytes and filamentous algae, had a greater estimated density and biomass of invertebrates and fishes).

A comparison of invertebrate and fish assemblages between rivers provided insight into community level changes that may occur if macrophytes are lost from a system. Species that rely on vegetation for foraging, refuge or reproduction will likely be negatively affected by large-scale habitat loss. For example, I estimated greater densities and biomass of multiple freshwater species in the Chassahowitzka River, including crayfish (Camp et al. 2011), grass shrimp (Camp et al. 2011), rainwater killifish, bluefin killifish, *Notropis* spp., spotted sunfish, lake chubsucker and largemouth bass, that were less abundant in the Homosassa River. Furthermore, I documented large cohorts of fishes surviving to older age classes in the Chassahowitzka River over the study period. In the Homosassa River, cohorts of age-0 largemouth bass and spotted sunfish were observed; however, few individuals were captured in subsequent sampling events at older age classes, contrary to observations in the Chassahowitzka River (unpublished data). Few age-0 lake chubsucker were captured in the Homosassa River during the first sampling event and none were captured in the study reaches during the following sampling periods with the exception of June 2010 following high production of filamentous algae in March and April 2010. I observed the greatest densities of juvenile and small-bodied fishes in Reach 1 of the Homosassa River during June 2010, subsequent to the increased production of filamentous algae. These data indicate that macrophytes may be important for recruitment of many species in coastal rivers by providing year-round forage and refuge habitat for larvae and juveniles.

Historic observations of the fish community in the Homosassa River (Herald and Strickland 1949) indicated that select phytophilic species were once common, but my results showed that these species have been nearly extirpated from reaches where macrophyte loss has been substantial. Lake chubsucker and *Notropis* spp., specifically, were observed in the Homosassa River prior to macrophyte loss (Herald and Strickland 1949); however, I rarely encountered either of these species over the period of study.

Although baseline data on the fish communities within coastal rivers are sparse, this qualitative comparison of fish community composition prior to large-scale habitat loss corroborates the assertion that macrophytes provide essential habitat for phytophilic species, and that the loss of this key habitat component may result in the decline or extirpation of these taxa. Similar patterns of fish community effects were observed by Whitfield (1986) after the loss of aquatic macrophytes in a coastal lake, Bettoli et al. (1993) following the removal of aquatic vegetation from a reservoir community, and Deegan et al. (2002) from experimental habitat manipulations in seagrass communities.

The spatial and temporal comparisons of the aquatic communities within the Chassahowitzka and Homosassa rivers demonstrated how loss of a key habitat component may affect multiple trophic groups. Macrophytes provide predation refuge for small-bodied fishes and invertebrates, such as *Notropis* spp. and aquatic insects; create a substrate for the colonization and production of periphyton which serves as a food base for chubsuckers and grass shrimp; and contribute to the detrital base which is utilized by crayfish and detritivorous fishes, such as striped mullet. In contrast, filamentous algae and its associated periphyton provides habitat for grazing amphipods and other invertebrates, which I observed in greater biomass during periods of increased filamentous algae production, despite higher densities of saltwater fish predators. The extirpation of macrophytes and replacement with filamentous algae production may have cascading food web effects, resulting in an altered community structure dependent on benthic and algal food bases.

Table 3-1. Mean estimated biomass (g·100 m^{-2}) of plants, algae, invertebrates and fishes within the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka		Homosassa	
	Summer	Winter	Summer	Winter
Vascular plants	116,532	89,693	942	1,262
Filamentous algae	6,917	53,147	13,730	39,418
Periphyton[1]	29,133	22,423	NA	NA
Sediment diatoms[2]	26,289	NA	NA	NA
Sediments invertebrates	67	166	41	493
Vegetation invertebrates	315	578	103	5,023
Amphipods	189	2,316	191	1,562
Crayfish[3]	2,270	474	0	0
Blue crab[3]	613	1,518	0	529
Mud crab[3]	176	38	251	3,865
Shrimp[3]	532	315	0	42
Juvenile lake chubsucker	3	11	0	0
Adult lake chubsucker	42	24	0	0
Small-bodied freshwater fishes	795	16	305	39
Juvenile *Lepomis* spp.	7	14	8	7
Adult *Lepomis* spp.	204	225	59	29
Gar	1	0	36	25
American eel	42	29	53	41
Juvenile largemouth bass	7	23	18	7
Adult largemouth bass	510	255	128	61
Striped mullet	131	15	105	107
Small-bodied saltwater fishes	890	440	1,643	1,218
Pinfish	160	108	32	8
Sheepshead	1	1	19	8
Gray snapper	5	1,066	50	1,064
Catfish	0	0	2	1
Red drum	0	0	3	7
Common snook	15	0	23	72

[1]Frazer et al. 2006, [2]Frazer unpublished data, [3]Camp et al. 2011

Table 3-2. Freshwater fish species captured within the Chassahowitzka River, Florida.

Scientific Name	Common Name
Ameiurus natalis	Yellow bullhead
Ameiurus nebulosus	Brown bullhead
Anguilla rostrata	American eel
Cyprinodon variegatus	Sheepshead minnow
Erimyzon sucetta	Lake chubsucker
Fundulus seminolis	Seminole killifish
Gambusia holbrooki	Eastern mosquitofish
Heterandria formosa	Least killifish
Lepisosteus osseus	Longnose gar
Lepisosteus platyrhincus	Florida gar
Lepomis gulosus	Warmouth
Lepomis macrochirus	Bluegill
Lepomis microlophus	Redear sunfish
Lepomis punctatus	Spotted sunfish
Lucania goodei	Bluefin killifish
Lucania parva	Rainwater killifish
Menidia beryllina	Inland silverside
Micropterus salmoides	Largemouth bass
Notemigonus crysoleucas	Golden shiner
Notropis harperi	Redeye chub
Notropis petersoni	Coastal shiner
Poecilia latipinna	Sailfin molly

Table 3-3. Saltwater fish species captured within the Chassahowitzka River, Florida.

Scientific Name	Common Name
Anchoa mitchilli	Bay anchovy
Archosargus probatocephalus	Sheepshead
Ariopsis felis	Hardhead catfish
Bairdiella chrysoura	Silver perch
Brevoortia sp.	Menhaden
Caranx hippos	Crevalle jack
Centropomus undecimalis	Common snook
Cynoscion nebulosus	Spotted seatrout
Dasyatis sp.	Stingray
Elops saurus	Ladyfish
Eucinostomus harengulus	Tidewater mojarra
Eucinostomus gula	Silver jenny
Fundulus confluentus	Marsh killifish
Fundulus grandis	Gulf killifish
Gobiosoma bosc	Naked goby
Lagodon rhomboides	Pinfish
Leiostomus xanthurus	Spot
Lutjanus griseus	Gray snapper
Microgobius gulosus	Clown goby
Mugil cephalus	Striped mullet
Mugil curema	White mullet
Oligoplites saurus	Leatherjacket
Opsanus beta	Gulf toadfish
Sciaenops ocellatus	Red drum
Strongylura marina	Atlantic needlefish
Strongylura notata	Redfin needlefish
Strongylura timucu	Timucu
Syngnathus scovelli	Gulf pipefish
Synodus foetens	Lizardfish
Trinectes maculatus	Hogchoker

Table 3-4. Freshwater fish species captured within the Homosassa River, Florida.

Scientific Name	Common Name
Ameiurus natalis	Yellow bullhead
Ameiurus nebulosus	Brown bullhead
Anguilla rostrata	American eel
Cyprinodon variegatus	Sheepshead minnow
Erimyzon sucetta	Lake chubsucker
Esox niger	Chain pickerel
Fundulus seminolis	Seminole killifish
Gambusia holbrooki	Eastern mosquitofish
Heterandria formosa	Least killifish
Lepisosteus osseus	Longnose gar
Lepisosteus platyrhincus	Florida gar
Lepomis macrochirus	Bluegill
Lepomis microlophus	Redear sunfish
Lepomis punctatus	Spotted sunfish
Lucania goodei	Bluefin killifish
Lucania parva	Rainwater killifish
Menidia beryllina	Inland silverside
Micropterus salmoides	Largemouth bass
Notemigonus crysoleucas	Golden shiner
Notropis harperi	Redeye chub
Notropis petersoni	Coastal shiner
Poecilia latipinna	Sailfin molly

Table 3-5. Saltwater fish species captured within the Homosassa River, Florida.

Scientific Name	Common Name
Anchoa mitchilli	Bay anchovy
Archosargus probatocephalus	Sheepshead
Ariopsis felis	Hardhead catfish
Bagre marinus	Gafftopsail catfish
Bairdiella chrysoura	Silver perch
Brevoortia sp.	Menhaden
Caranx hippos	Crevalle jack
Centropomus undecimalis	Common snook
Cynoscion nebulosus	Spotted seatrout
Dasyatis sp.	Stingray
Eugerres plumieri	Striped mojarra
Echeneis sp.	Sharksucker
Elops saurus	Ladyfish
Eucinostomus gula	Silver jenny
Eucinostomus harengulus	Tidewater mojarra
Fundulus confluentus	Marsh killifish
Fundulus grandis	Gulf killifish
Gobiosoma bosc	Naked goby
Lagodon rhomboides	Pinfish
Leiostomus xanthurus	Spot
Lutjanus griseus	Gray snapper
Microgobius gulosus	Clown goby
Mugil cephalus	Striped mullet
Mugil curema	White mullet
Oligoplites saurus	Leatherjacket
Opsanus beta	Gulf toadfish
Pogonias cromis	Black drum
Sciaenops ocellatus	Red drum
Sphyraena barracuda	Barracuda
Strongylura marina	Atlantic needlefish
Strongylura notata	Redfin needlefish
Strongylura timucu	Timucu
Syngnathus scovelli	Gulf pipefish
Synodus foetens	Lizardfish
Trinectes maculatus	Hogchoker

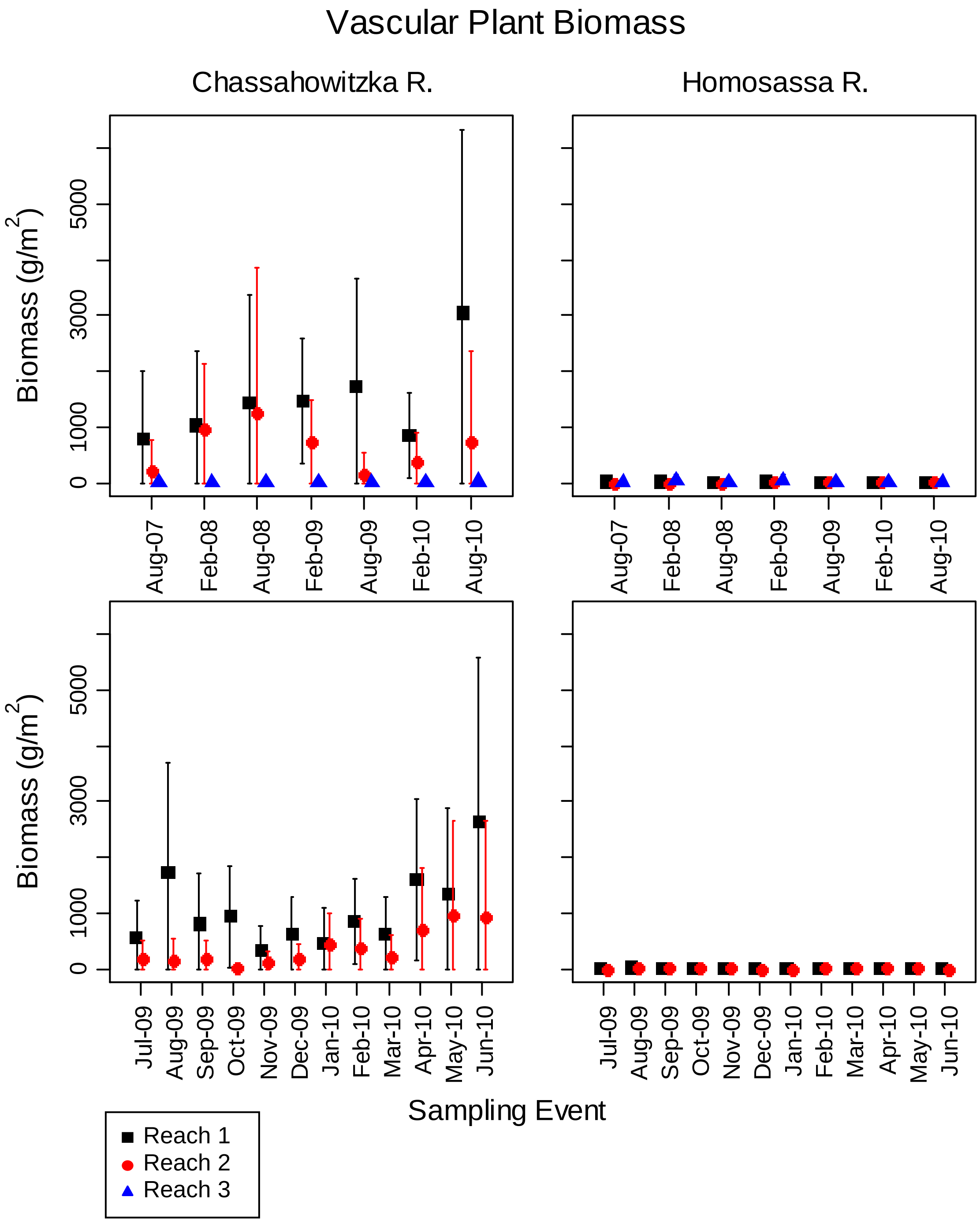

Figure 3-1. Average biomass (g·m^{-2} ± SD) of macrophytes within the Chassahowitzka and Homosassa rivers during August 2007 through August 2010 (n=15 samples per reach in each river). Biannual time series are shown for the period of study and monthly time series are shown for year three.

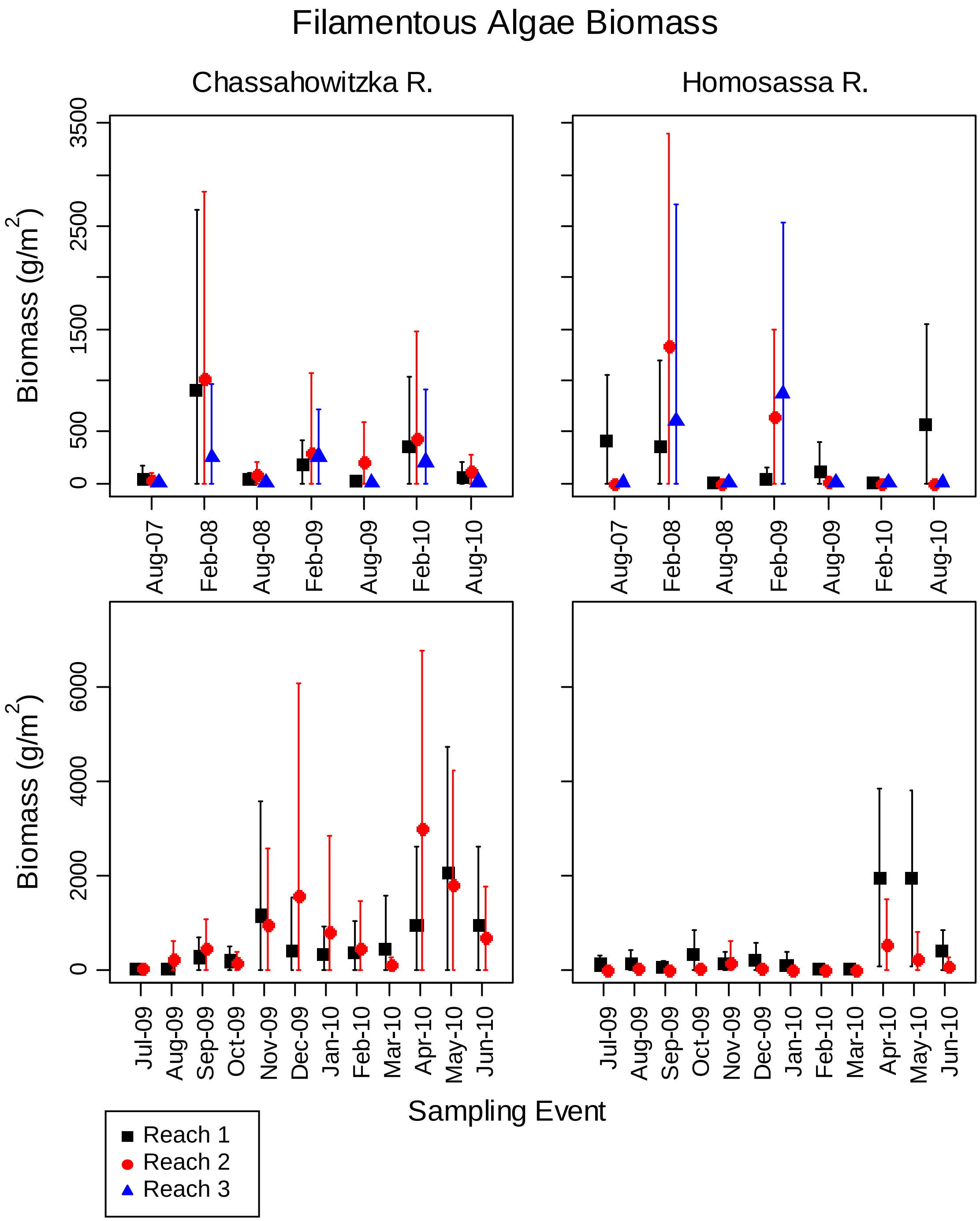

Figure 3-2. Average biomass (g·m^{-2} ± SD) of filamentous algae within the Chassahowitzka and Homosassa rivers during August 2007 through August 2010 (n=15 samples per reach in each river). Biannual time series are shown for the period of study and monthly time series are shown for year three.

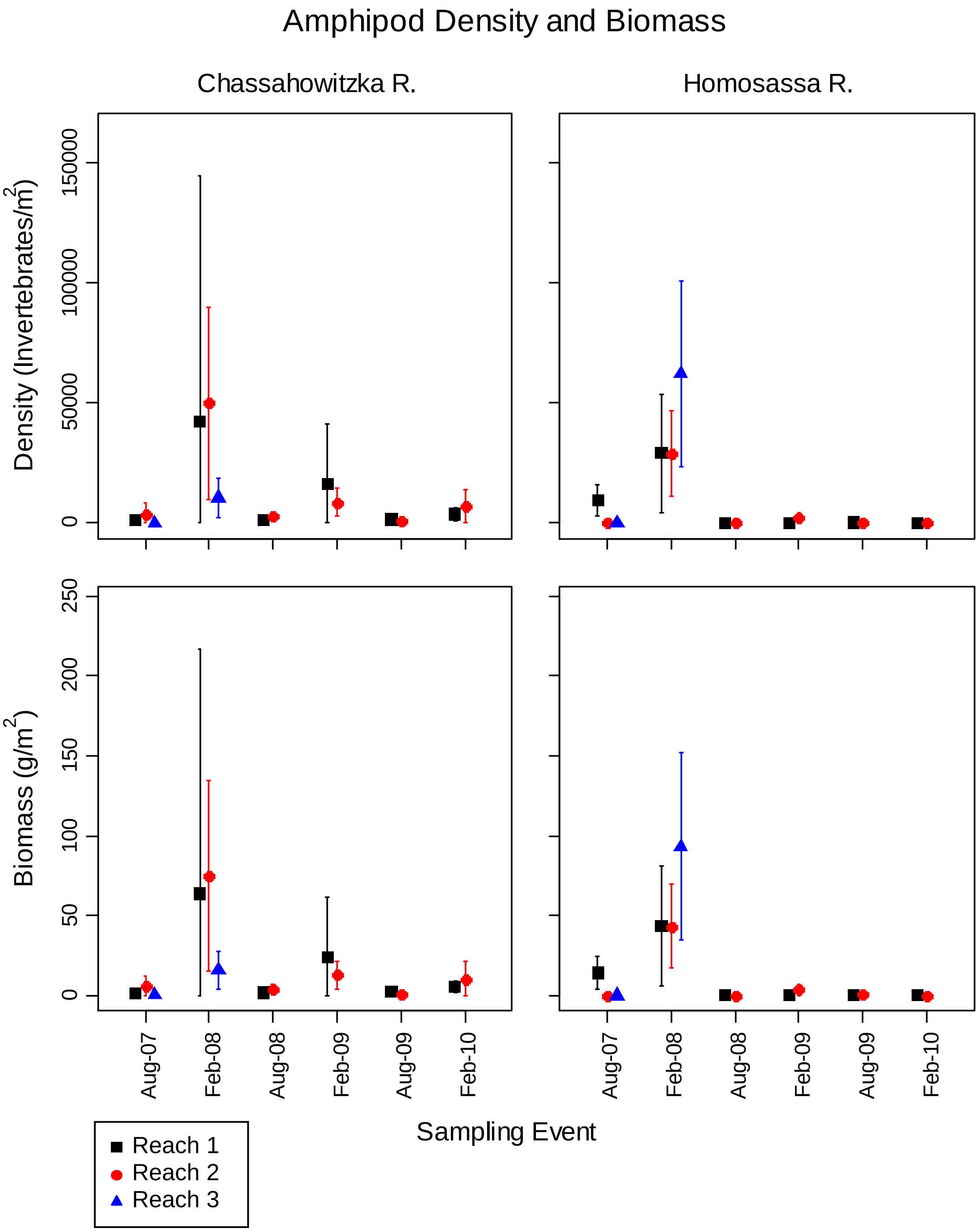

Figure 3-3. Average density (invertebrates·m^{-2} ± SD) and biomass (g·m^{-2} ± SD) of amphipods within the Chassahowitzka and Homosassa rivers during August 2007 through February 2010.

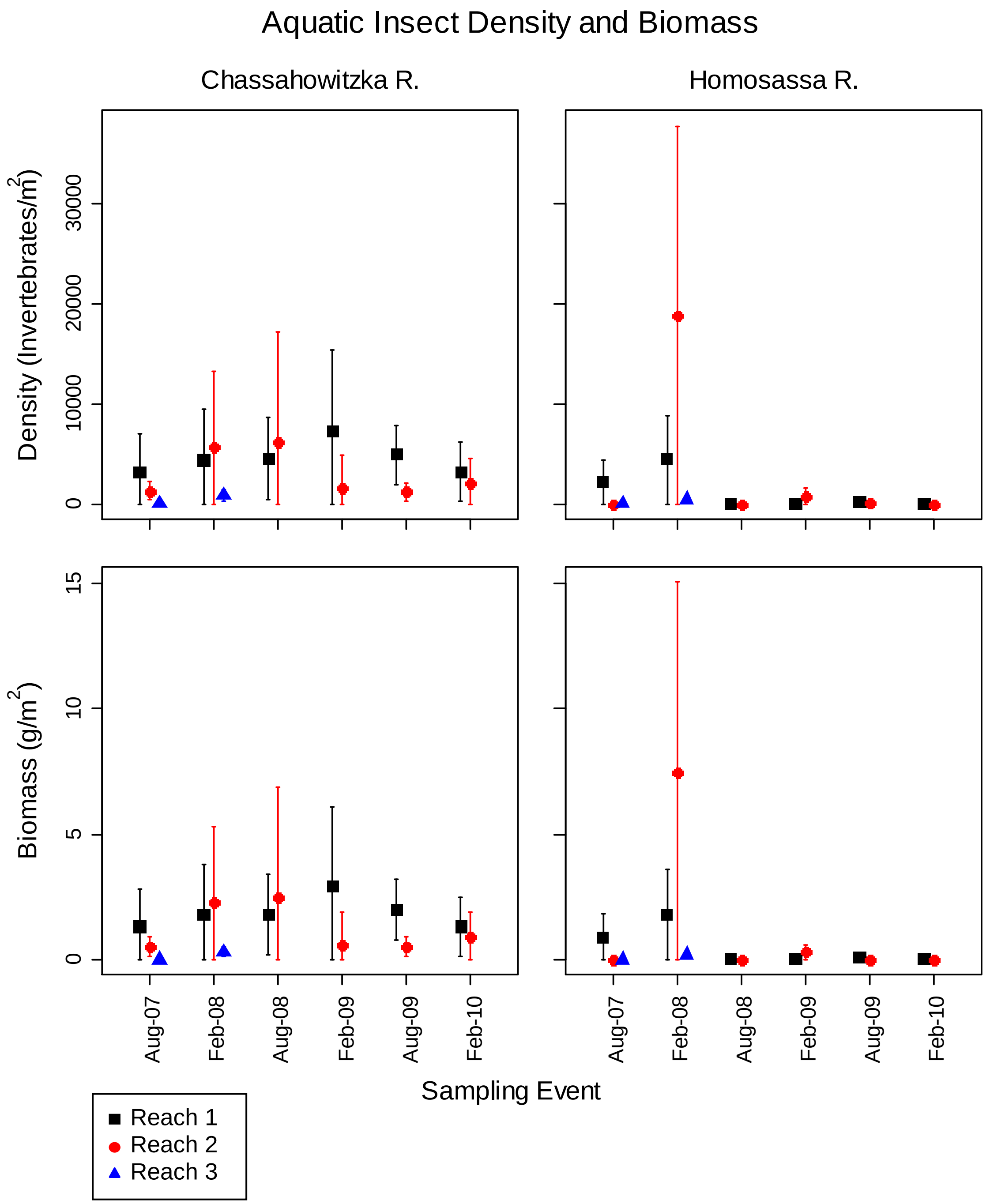

Figure 3-4. Average density (invertebrates·m^{-2} ± SD) and biomass (g·m^{-2} ± SD) of aquatic insects within the Chassahowitzka and Homosassa rivers during August 2007 through February 2010.

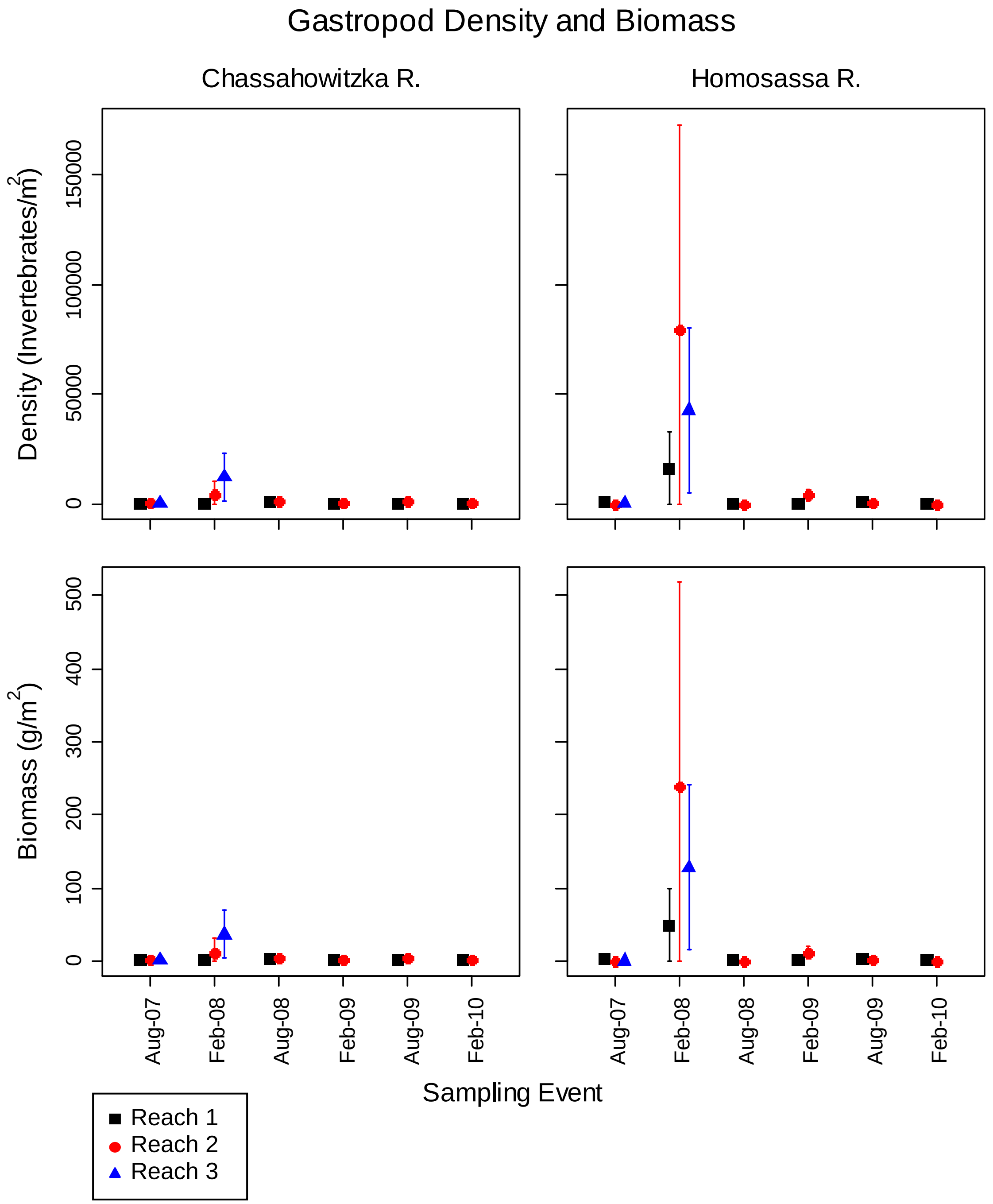

Figure 3-5. Average density (invertebrates·m^{-2} ± SD) and biomass (g·m^{-2} ± SD) of gastropods within the Chassahowitzka and Homosassa rivers during August 2007 through February 2010.

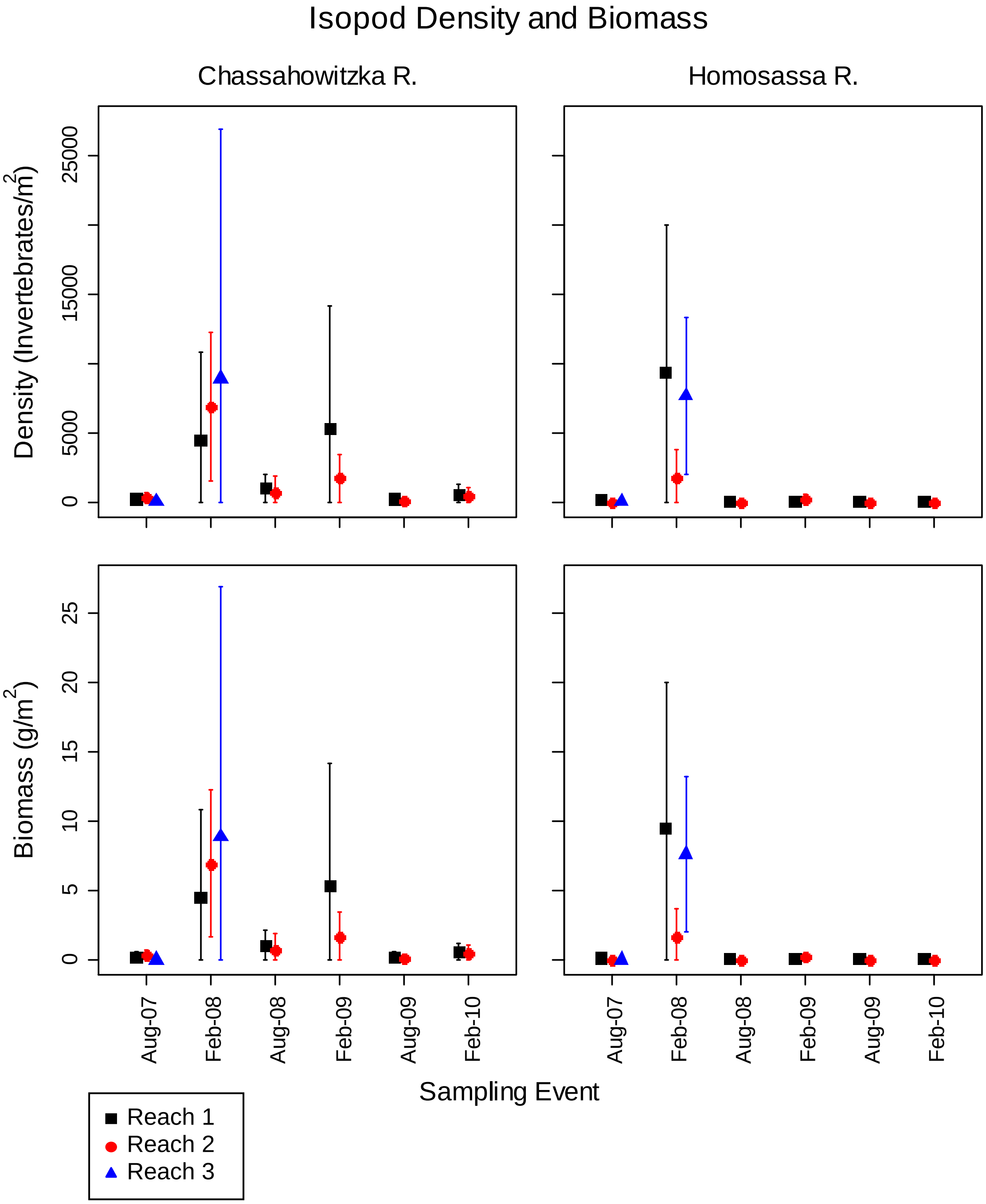

Figure 3-6. Average density (invertebrates·m^{-2} ± SD) and biomass (g·m^{-2} ± SD) of isopods within the Chassahowitzka and Homosassa rivers during August 2007 through February 2010.

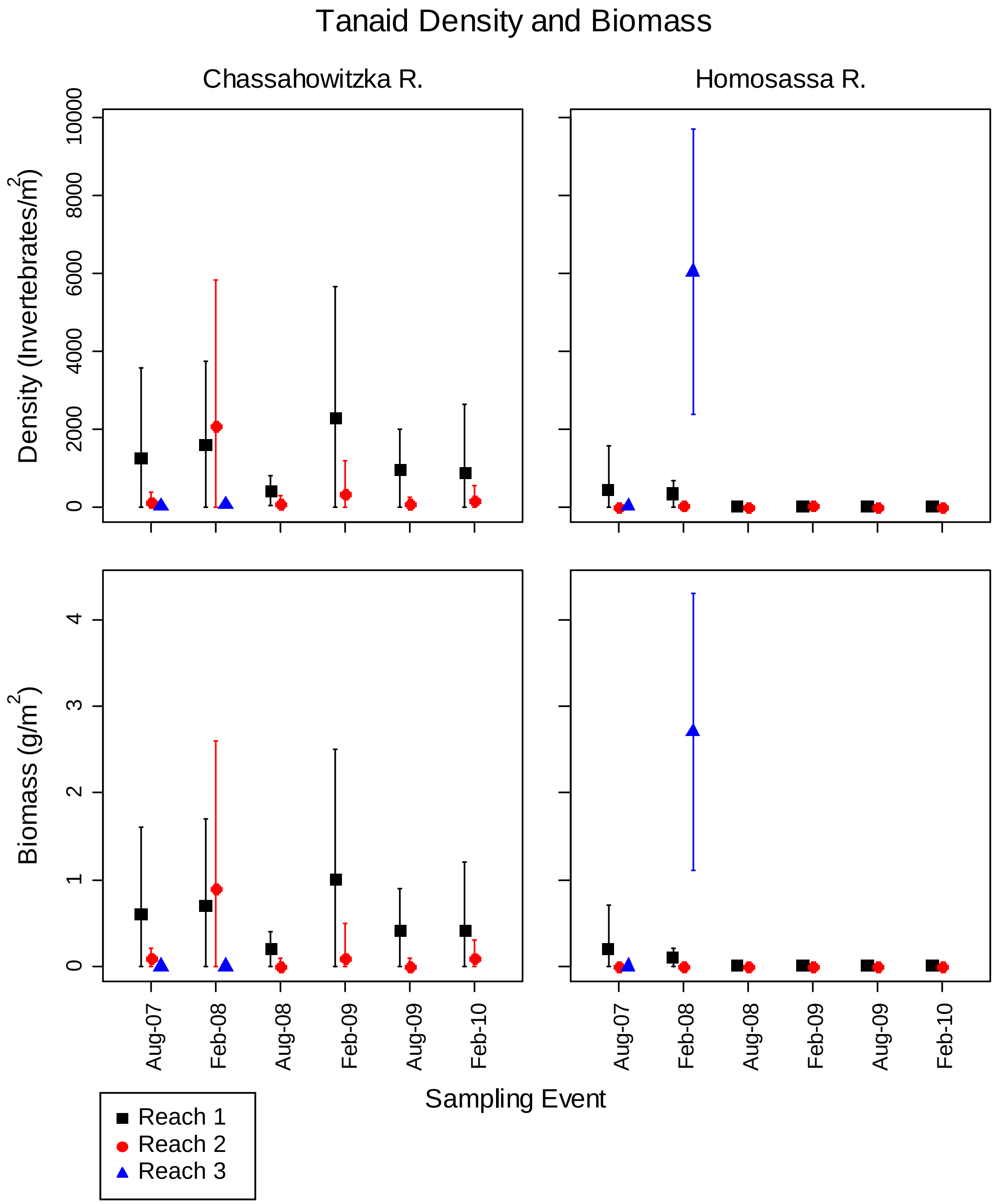

Figure 3-7. Average density (invertebrates·m^{-2} ± SD) and biomass (g·m^{-2} ± SD) of tanaids within the Chassahowitzka and Homosassa rivers during August 2007 through February 2010.

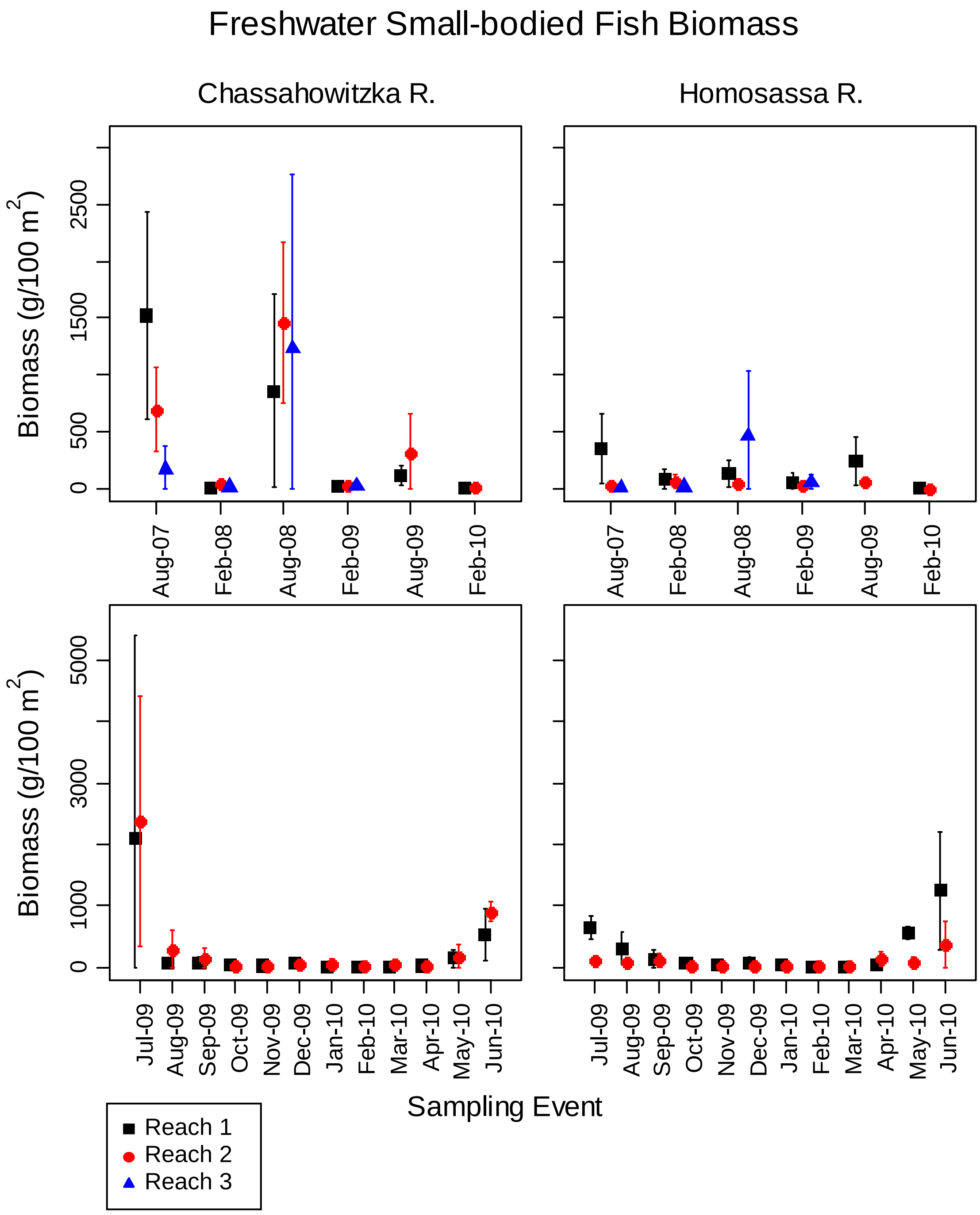

Figure 3-8. Average biomass (g·100 m^{-2} ± SD) of freshwater small-bodied fishes collected at seine depletion sites within the Chassahowitzka and Homosassa rivers. Biannual time series are shown for the period of study and monthly time series are shown for year three.

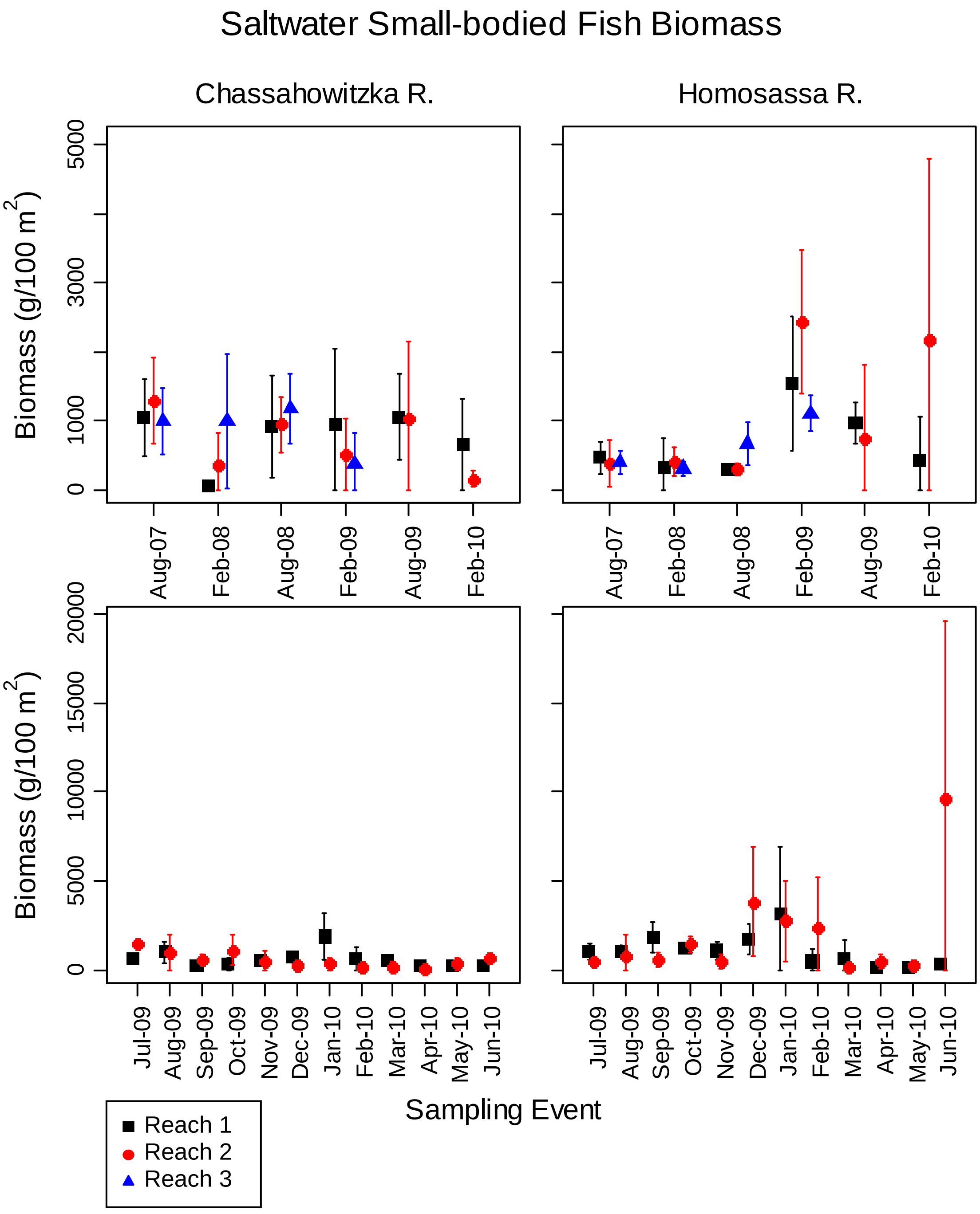

Figure 3-9. Average biomass (g·100 m^{-2} ± SD) of saltwater small-bodied fishes collected at seine depletion sites within the Chassahowitzka and Homosassa rivers. Biannual time series are shown for the period of study and monthly time series are shown for year three.

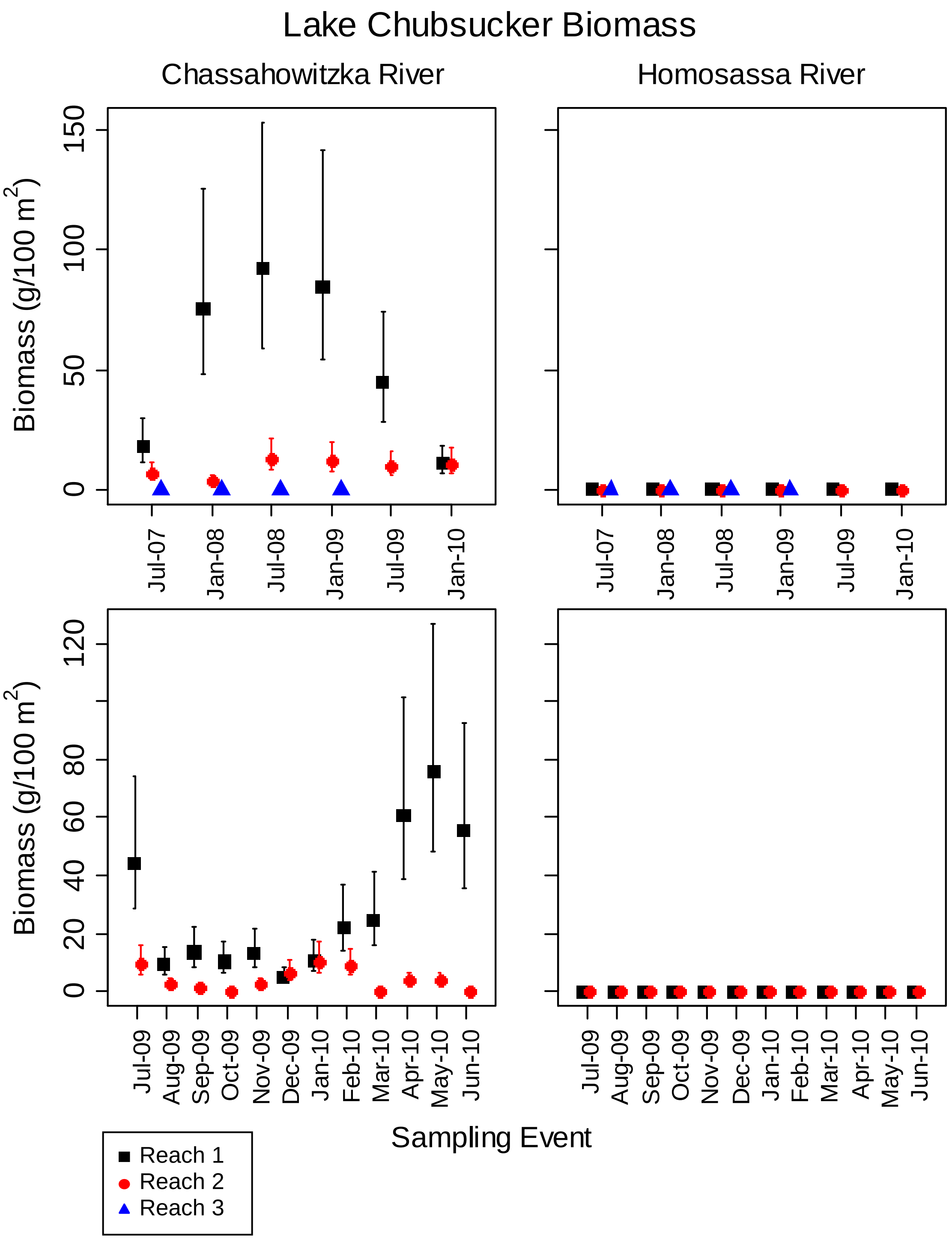

Figure 3-10. Estimated mean biomass (g·100 m^{-2}) of lake chubsucker captured during mark-recapture electrofishing sampling within the Chassahowitzka and Homosassa rivers. Error bars represent 95% confidence intervals of the mean. Biannual time series are shown for the period of study and monthly time series are shown for year three.

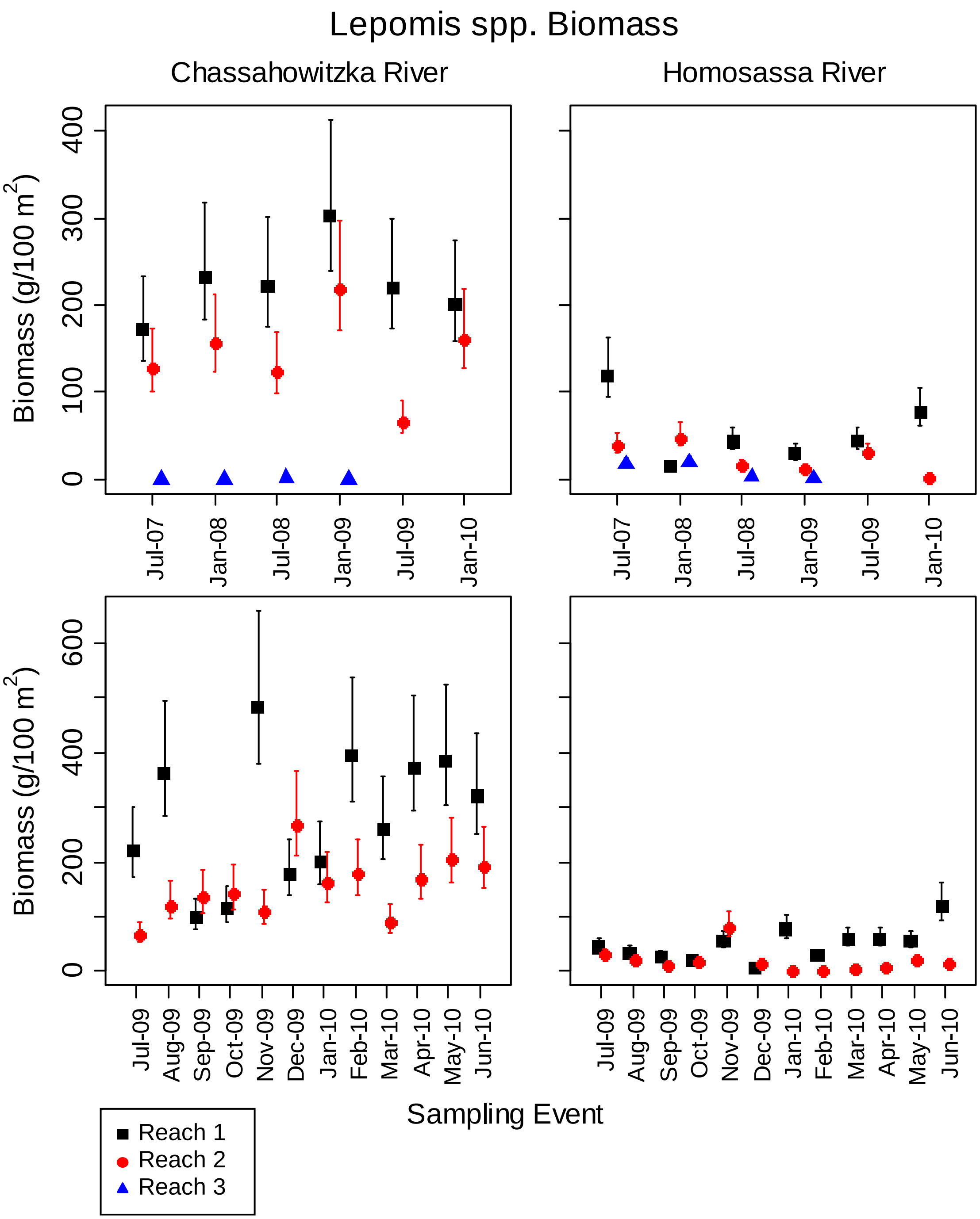

Figure 3-11. Estimated mean biomass (g·100 m^{-2}) of *Lepomis* spp. captured during mark-recapture electrofishing sampling within the Chassahowitzka and Homosassa rivers. Error bars represent 95% confidence intervals of the mean. Biannual time series are shown for the period of study and monthly time series are shown for year three.

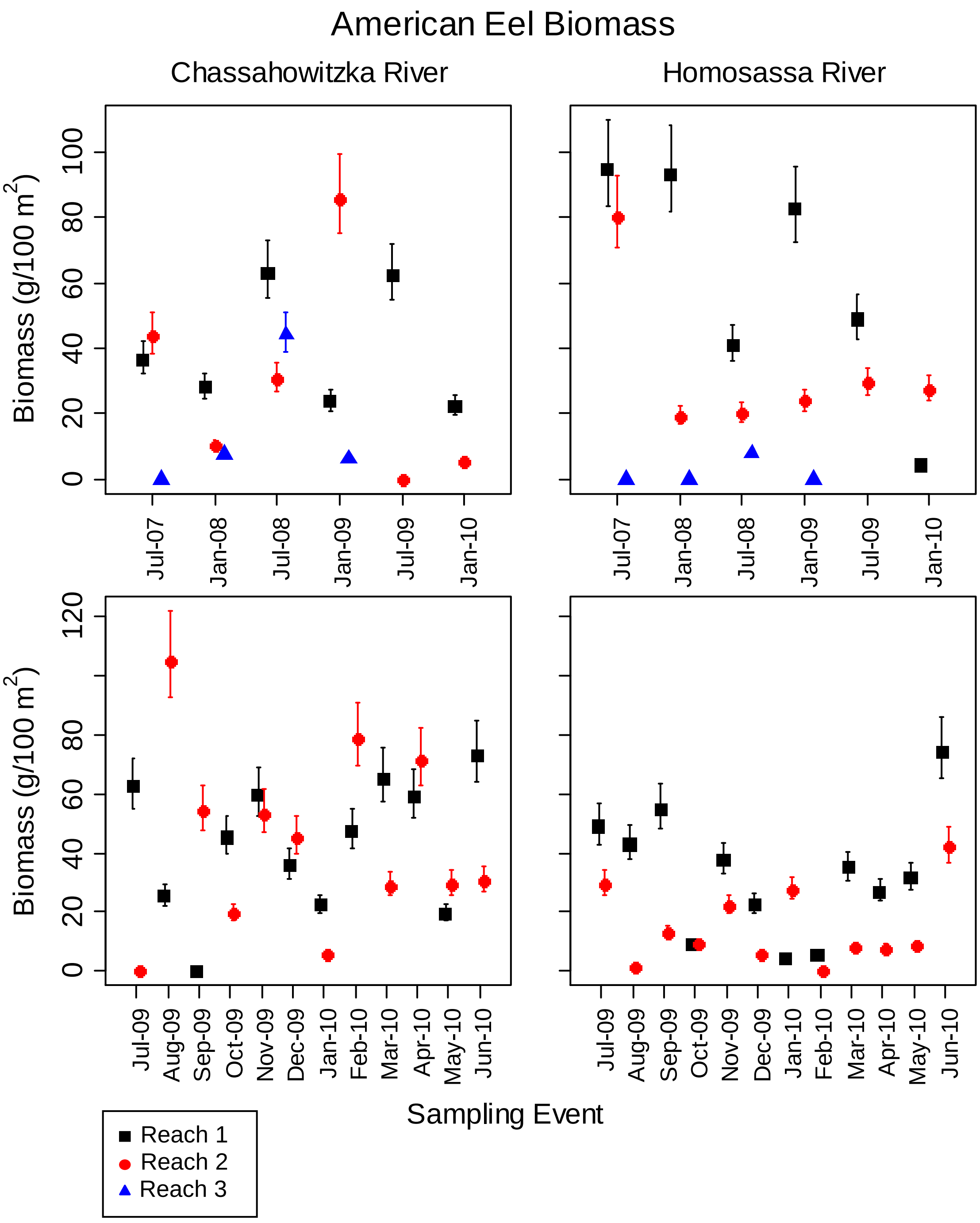

Figure 3-12. Estimated mean biomass (g·100 m^{-2}) of American eel captured during mark-recapture electrofishing sampling within the Chassahowitzka and Homosassa rivers. Error bars represent 95% confidence intervals of the mean. Biannual time series are shown for the period of study and monthly time series are shown for year three.

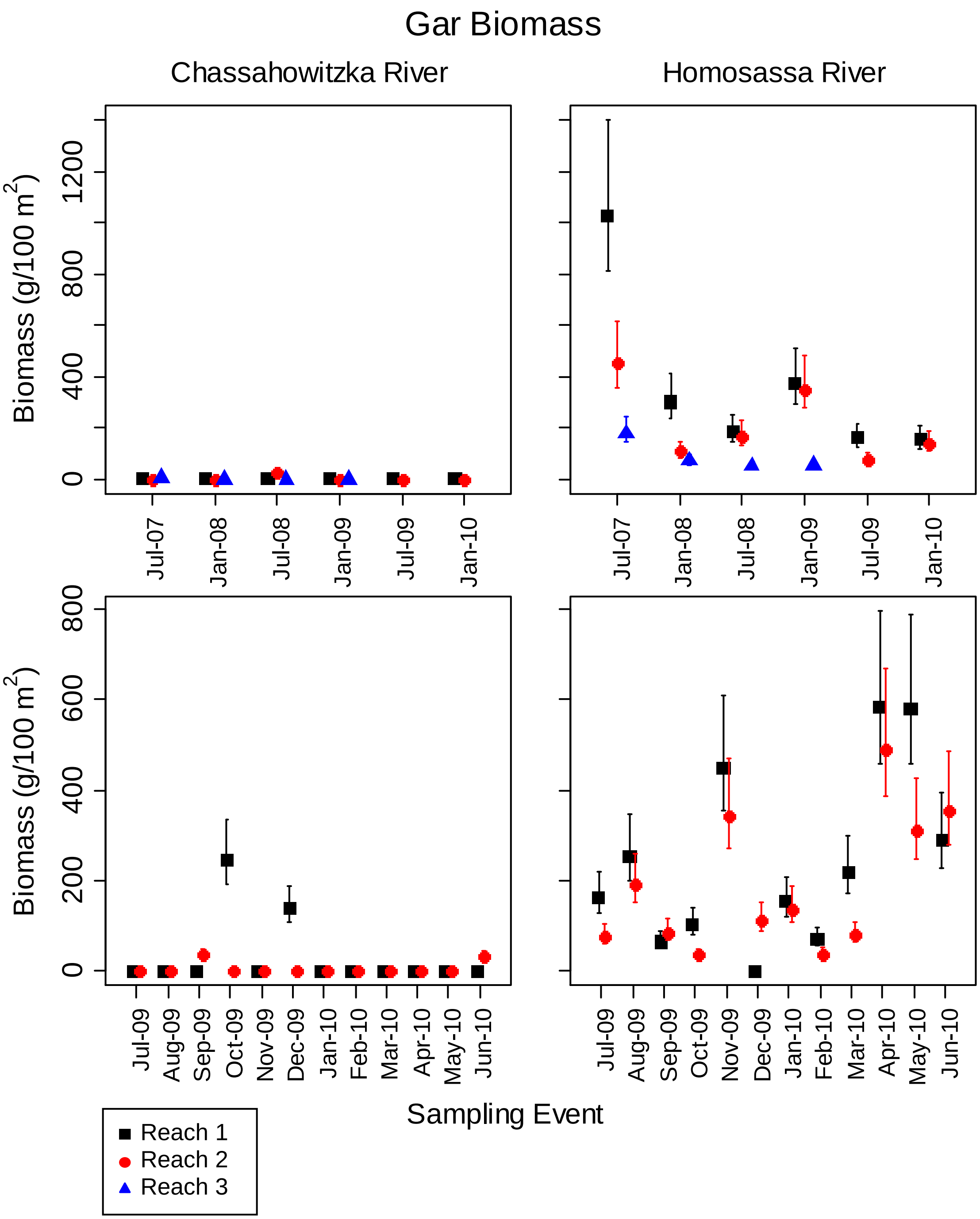

Figure 3-13. Estimated mean biomass (g·100 m^{-2}) of gar captured during mark-recapture electrofishing sampling within the Chassahowitzka and Homosassa rivers. Error bars represent 95% confidence intervals of the mean. Biannual time series are shown for the period of study and monthly time series are shown for year three.

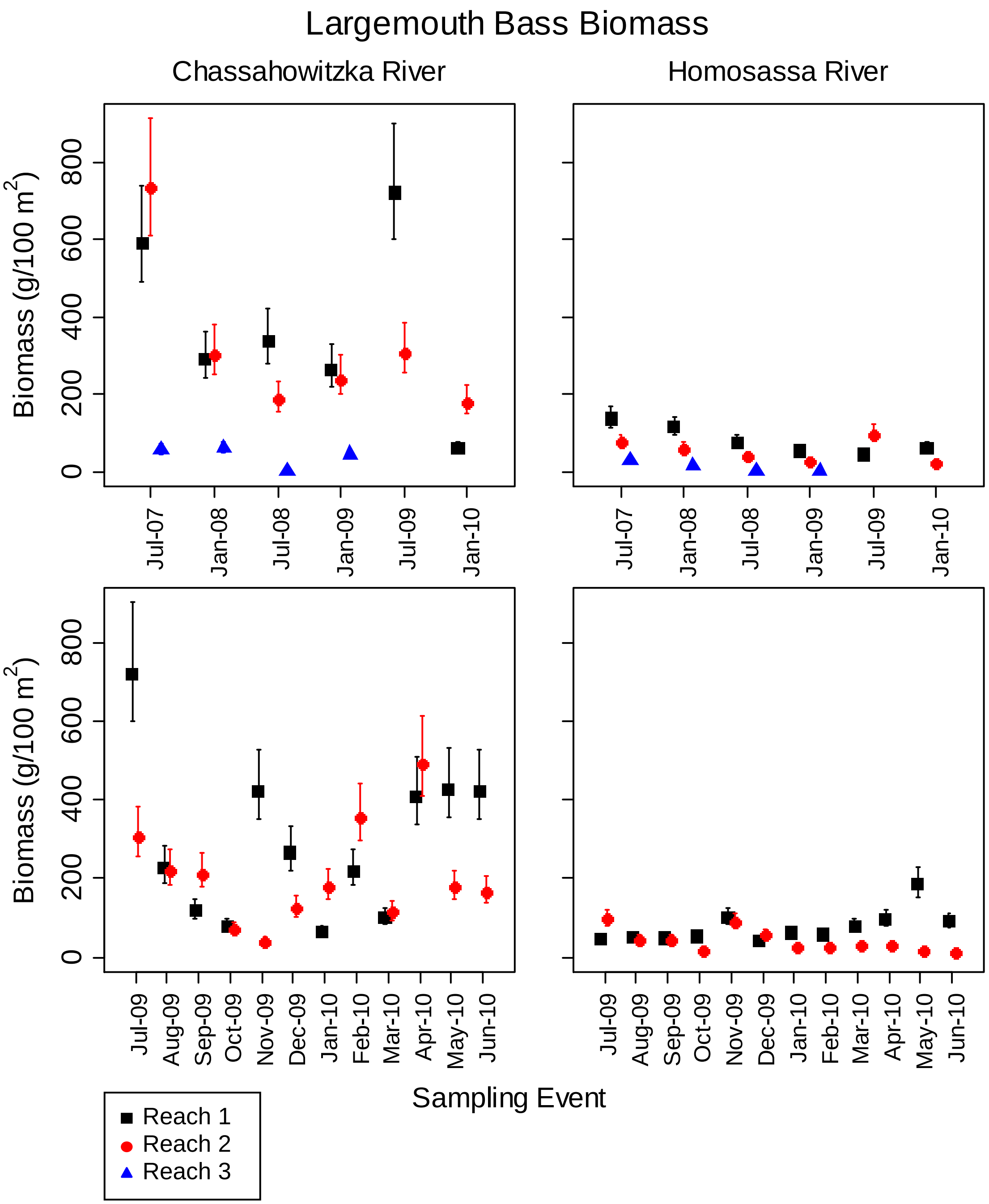

Figure 3-14. Estimated mean biomass (g·100 m^{-2}) of largemouth bass captured during mark-recapture electrofishing sampling within the Chassahowitzka and Homosassa rivers. Error bars represent 95% confidence intervals of the mean. Biannual time series are shown for the period of study and monthly time series are shown for year three.

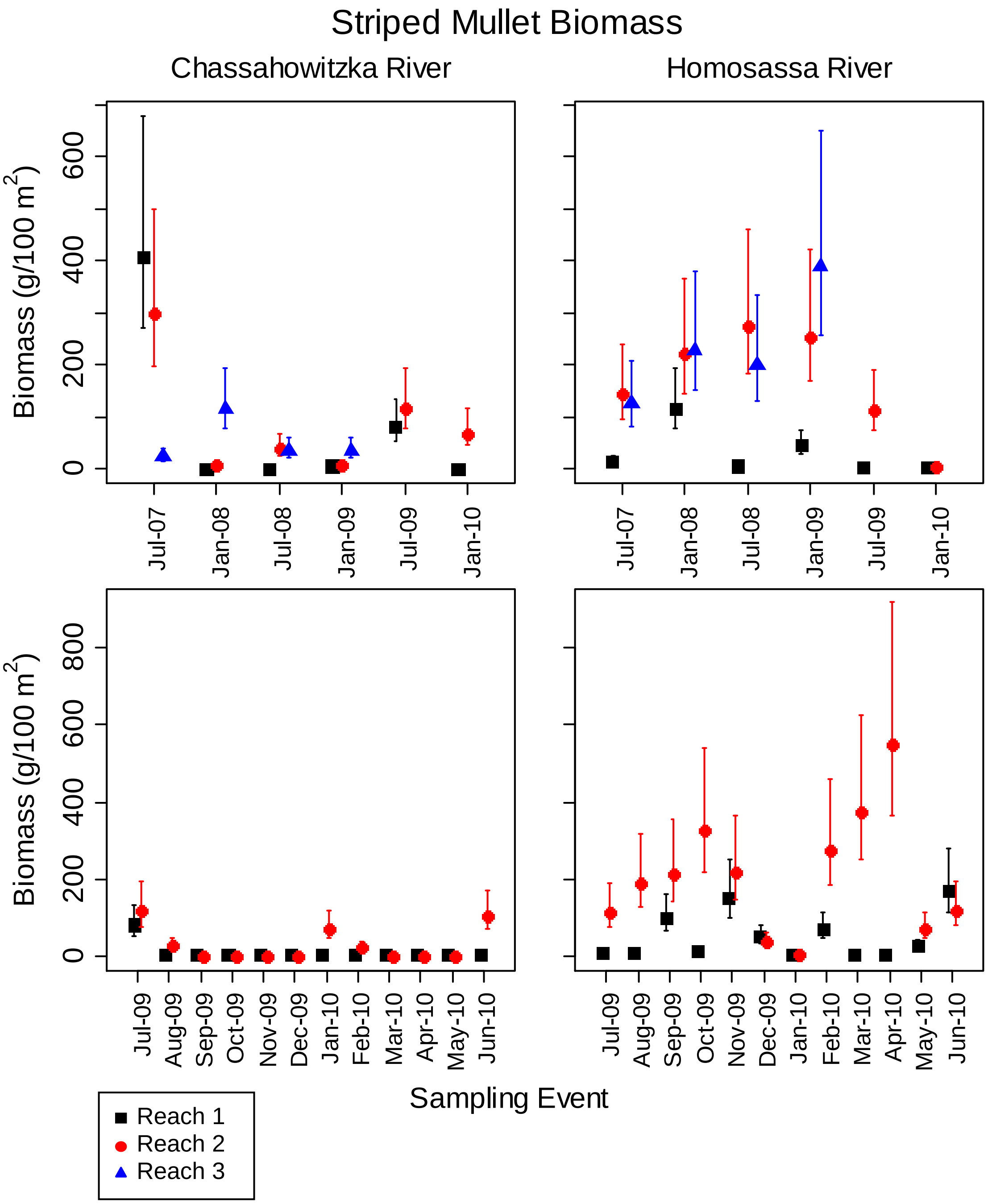

Figure 3-15. Estimated mean biomass (g·100 m^{-2}) of striped mullet captured during mark-recapture electrofishing sampling within the Chassahowitzka and Homosassa rivers. Error bars represent 95% confidence intervals of the mean. Biannual time series are shown for the period of study and monthly time series are shown for year three.

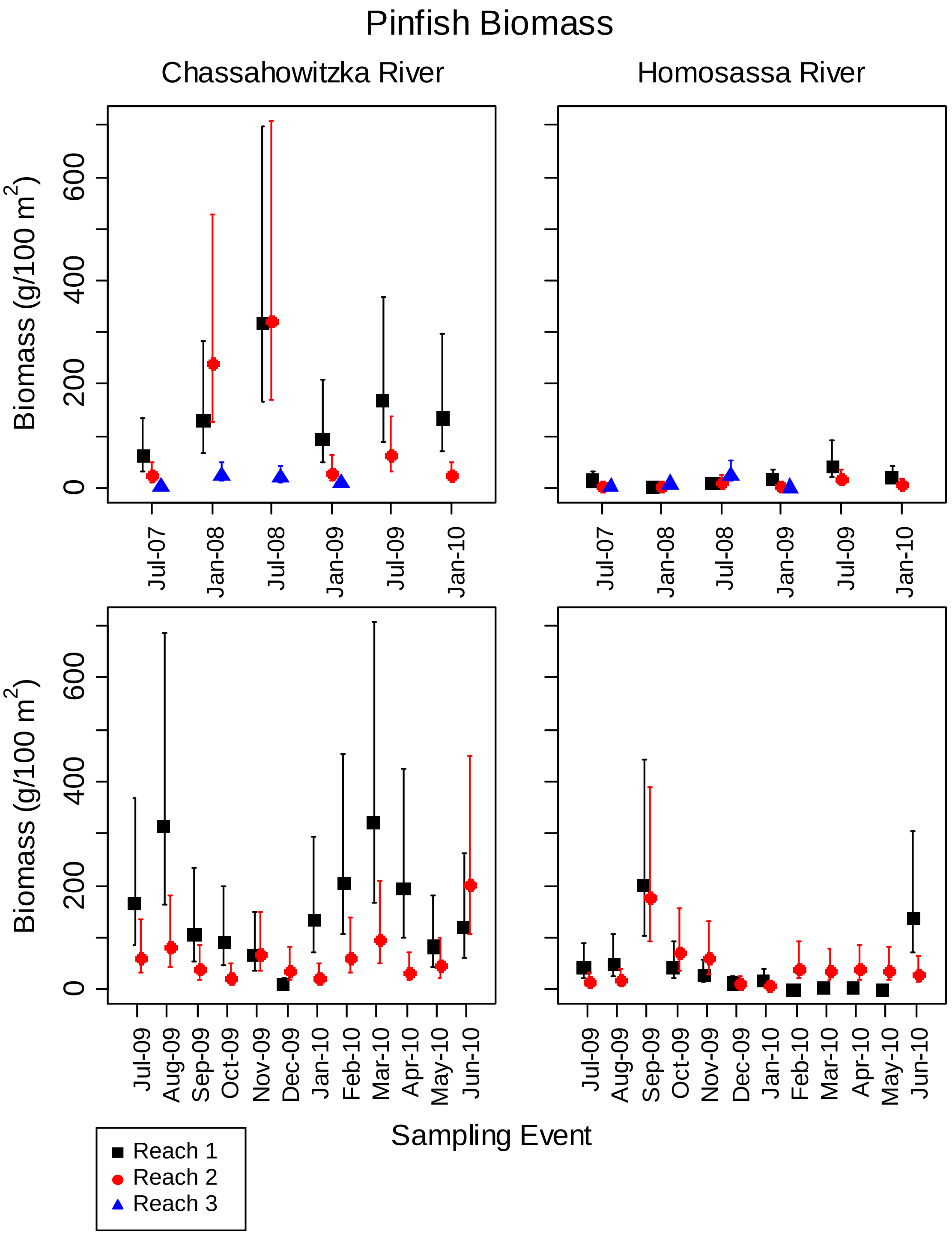

Figure 3-16. Estimated mean biomass (g·100 m^{-2}) of pinfish captured during mark-recapture electrofishing sampling within the Chassahowitzka and Homosassa rivers. Error bars represent 95% confidence intervals of the mean. Biannual time series are shown for the period of study and monthly time series are shown for year three.

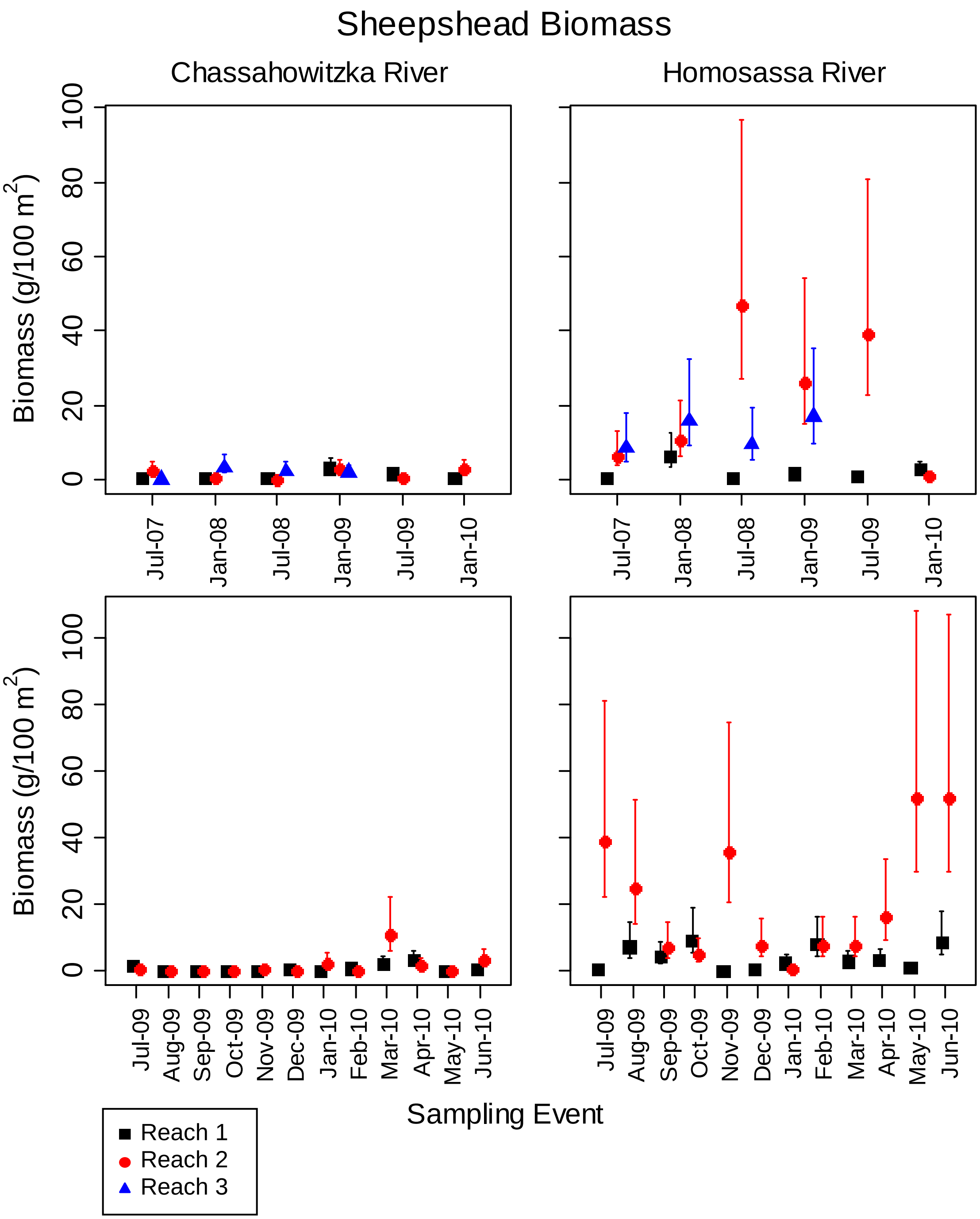

Figure 3-17. Estimated mean biomass (g·100 m^{-2}) of sheepshead captured during mark-recapture electrofishing sampling within the Chassahowitzka and Homosassa rivers. Error bars represent 95% confidence intervals of the mean. Biannual time series are shown for the period of study and monthly time series are shown for year three.

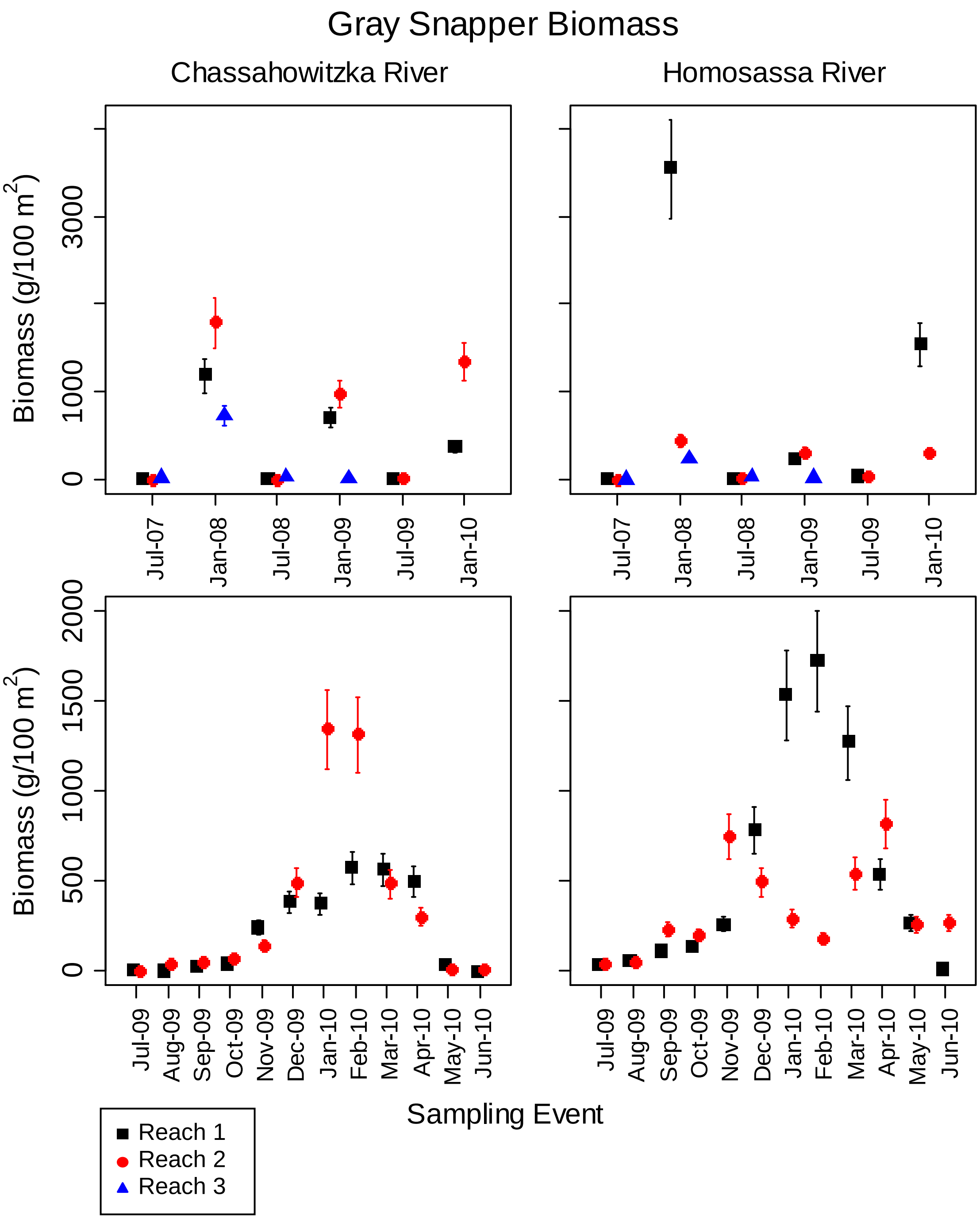

Figure 3-18. Estimated mean biomass (g·100 m^{-2}) of gray snapper captured during mark-recapture electrofishing sampling within the Chassahowitzka and Homosassa rivers. Error bars represent 95% confidence intervals of the mean. Biannual time series are shown for the period of study and monthly time series are shown for year three.

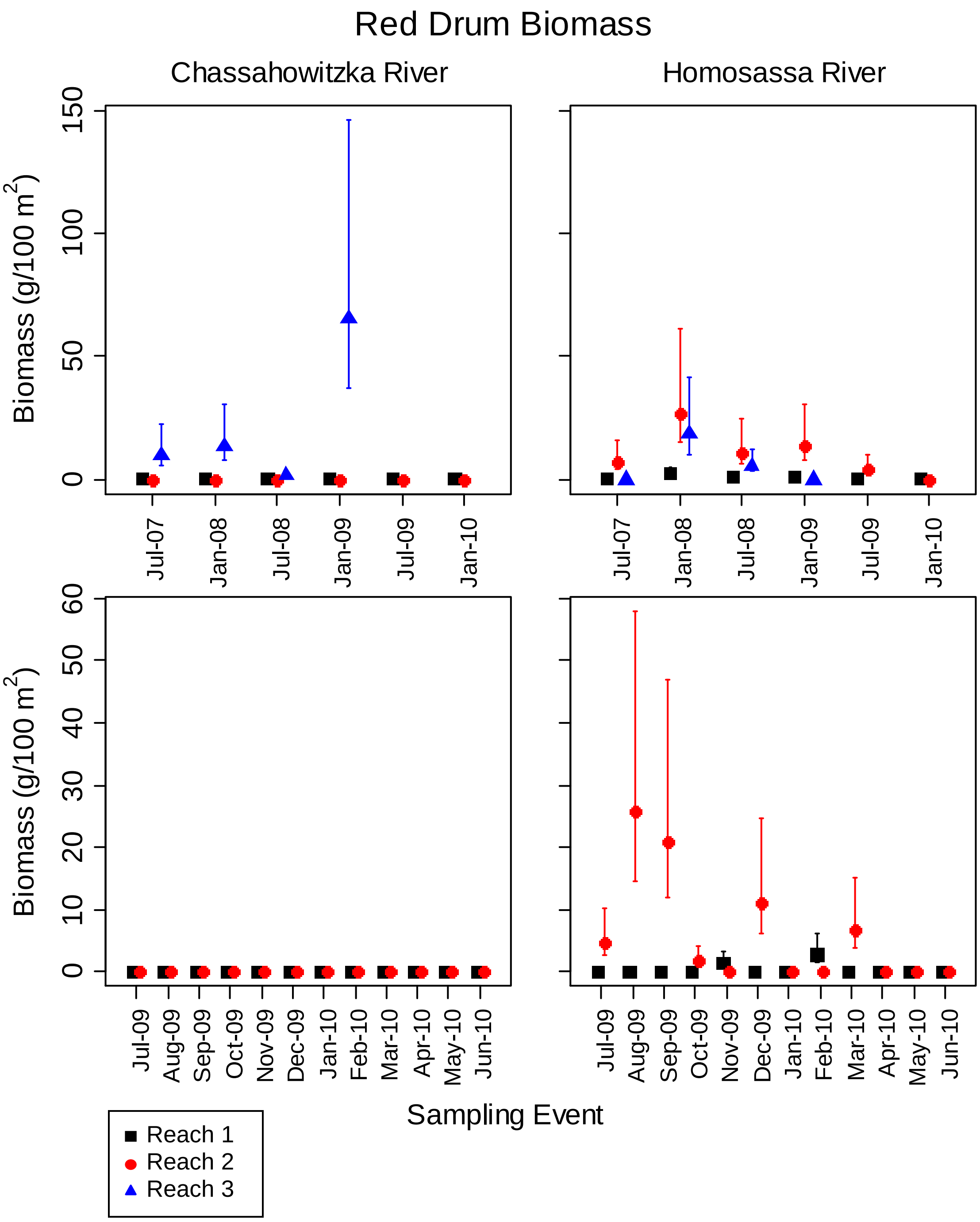

Figure 3-19. Estimated mean biomass (g·100 m^{-2}) of red drum captured during mark-recapture electrofishing sampling within the Chassahowitzka and Homosassa rivers. Error bars represent 95% confidence intervals of the mean. Biannual time series are shown for the period of study and monthly time series are shown for year three.

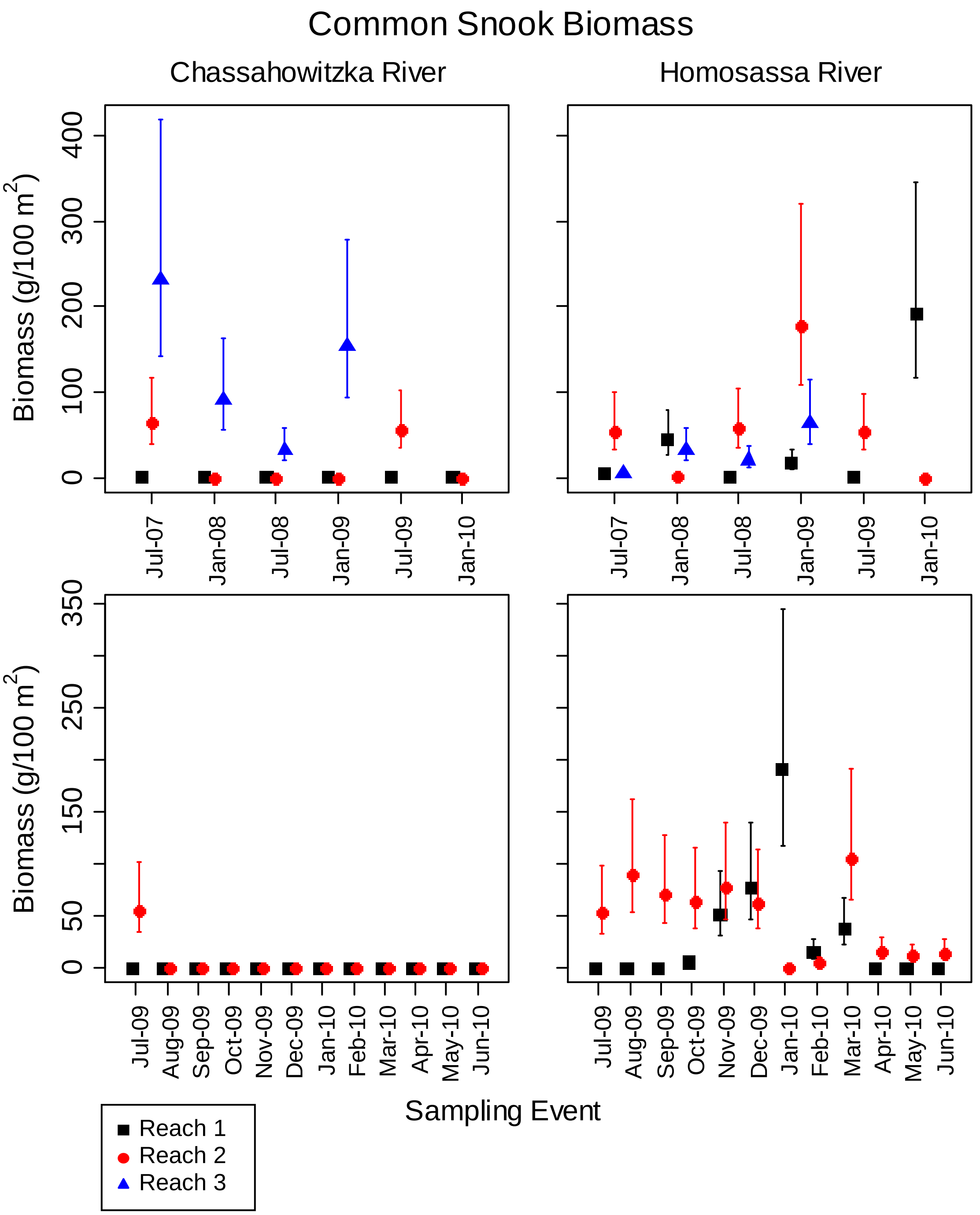

Figure 3-20. Estimated mean biomass (g·100 m^{-2}) of common snook captured during mark-recapture electrofishing sampling within the Chassahowitzka and Homosassa rivers. Error bars represent 95% confidence intervals of the mean. Biannual time series are shown for the period of study and monthly time series are shown for year three.

CHAPTER 4
THE DIET HABITS OF FRESHWATER AND MARINE FISHES IN COASTAL RIVERS

Introduction

Predator-prey interactions have been a central focus of ecology for nearly a century (Berryman 1992), and much ecological insight has been gained from examining how predators interact with their prey and vice versa. From the pioneering work of Lotka (1925) and Volterra (1931) in constructing differential equations mathematically describing predator-prey interaction to the development of more complex theories to account for behavioral responses (Holling 1959, Preisser et al. 2005), habitat spatial structure (Huffaker 1958, McArthur and Pianka 1966) and trophic cascades (Carpenter et al. 1985, Pace et al. 1999), the study of predation has provided valuable insight into principle factors that influence the distributions and densities of populations. Predators exert a strong control over prey populations through direct consumption and intimidation (Preisser et al. 2005), particularly in open water food webs (Carpenter and Kitchell 1996, Micheli 1999). Predator abundance and foraging is coupled to prey availability through density-dependent rates of reproduction, survival, consumption, or growth (Soloman 1949, Holling 1959, Murdoch 1971). Controlled experiments on predator-prey interactions have demonstrated that predators left unchecked can deplete prey populations, resulting in population crashes (Huffaker 1958) or prey switching (Murdoch 1969). For predator and prey species to coexist, systematic checks and balances must exist within ecosystems to prevent the rapid extinction of populations.

Prey species face the serious dilemma of acquiring enough food to grow and reproduce without being preyed upon while foraging (Walters and Martell 2004). This dilemma represents a behavioral trade-off between feeding in areas with available prey, and resting in habitats with lower predation risk (Gilliam and Fraser 1987, Walters and Martell 2004). The presence of predators can cause spatially distinct habitat use patterns of prey populations, including the avoidance of areas with high predator abundance (Preisser et al. 2005). This avoidance behavior can result in greater food resources for prey species in areas that overlap predators. Similarly, prey populations can quickly deplete food resources within refuge habitats, and must therefore move to areas with greater food availability to forage.

These coupled behavioral dynamics are often not effectively captured by mass-action models of predator-prey interaction (Walters and Martell 2004); however, models that incorporate predation vulnerability associated with spatially restricted foraging arenas (Walters and Juanes 1993, Walters and Martell 2004) have greatly improved the ability to predict population responses to changes in both food availability and predation. This predictive ability is useful for modeling food-web interactions and multispecies dynamics in aquatic ecosystems and predicting ecosystem responses to manipulations in predators (i.e. top down, fishing), prey (i.e. bottom-up, prey composition and abundance), or ecosystem attributes that may impact predator-prey dynamics (e.g., habitat structure) (Christensen and Pauly 1993, Walters and Martell 2004). Quantitative characterization of predator-prey interactions is central to trophic dynamic models aimed at understanding population- and community-level effects of changes in producer and consumer populations. If such interactions can be accurately characterized, then predictive models can be developed and used to assess and screen policy options related to managing and restoring ecosystems through manipulation of predators or prey populations directly (e.g., harvest regulations) or indirectly through mediating predator-prey interactions (e.g., habitat modification or restoration).

Habitat complexity has been shown to have large decoupling effects on predator-prey interactions within aquatic ecosystems. Highly structured habitats can inhibit predator foraging and decrease predation efficiency (Huffaker 1958, Crowder and Cooper 1982, Savino and Stein 1982), creating distinct refuge patches for prey species. Predators may aggregate and forage in patches containing a high availability of prey, and move to other, more profitable patches when prey populations become less abundant (Murdoch 1969, Valiela 1995). Patch connectivity allows for recolonization of depleted patches from densely populated ones. Within highly connected patches, the rate of colonization can offset the rate of predator depletion (local prey extinction). These patch dynamics can stabilize prey populations by lowering the probability of extinction (Fahrig and Merriam 1985, Namba et al. 1999).

Predation on individual prey species has been shown to be lower in ecosystems with highly heterogeneous habitats that support multiple prey populations due to lower predator encounter rate per prey species (Baalen et al. 2001). When prey encounters become rare, predators may exploit alternative populations that occur in greater abundance (Murdoch 1969). This prey switching behavior can increase the persistence of prey populations (Comins and Hassel 1975, van Baalen et al. 2001) as a result of decreased predation rates at low prey densities. Habitats that provide abundant food resources, low predation risk, and support a high diversity of prey species, are therefore thought to be important for maintaining predator and prey population viability. However, how predator communities respond to large-scale changes in habitat, and ultimately how this relates to predator-prey dynamics and ecosystem effects is most often assessed at small scales (aquaria or mesocosms) with few predators or prey (Jacobson and Berg 1989, Savino and Stein 1989), but has recently been expanded experimentally to small lakes (Sass et al. 2006). At larger spatial scales, manipulative experiments of predators, prey populations, and habitats may not be logistically feasible, particularly in lotic ecosystems. In these ecosystems, comparison of predator-prey interactions across spatially and temporally variably habitat availability and composition can provide insight into how predator populations respond to large-scale changes in habitat structure and prey availability.

An ecosystem study of coastal rivers in Florida provided an opportunity to assess how spatially and temporally dynamic changes in vegetative habitat affected the prey availability, composition, selectivity and foraging success of freshwater and marine fishes. Spring-fed, coastal rivers are unique, highly autochthonous ecosystems comprised of diverse communities of oligohaline and marine plants, algae, invertebrates and fishes (Herald and Strickland 1949, Odum 1953, Odum 1957). Several rivers along the west coast of Florida, including the Chassahowitzka and Homosassa rivers, historically supported dense assemblages of aquatic macrophytes; however, macrophyte fragmentation and loss have been significant during the last decade (Frazer et al. 2006). Currently, the Chassahowitzka River supports approximately half of the biomass of macrophytes compared to estimates from a decade ago, and nearly all macrophytes, including *Vallisneria americana*, *Potamogeton* spp., and *Sagittaria kurziana*, have declined significantly or been extirpated from the Homosassa River (Figure 4-1). Furthermore, large-scale seasonal blooms of filamentous algae, including

Chaetomorpha sp., *Gracilaria* sp., and *Lyngbya* sp., cover extensive portions of the riverbeds in late winter through spring (Figure 4-1). The Homosassa River is nearly devoid of aquatic vegetation during summer and fall months, whereas the Chassahowitzka supports macrophytes throughout the year. These plant and algae dynamics have resulted in structurally different and seasonally variable vegetative habitats within each river (Figure 4-1). Comparative analysis of predator-prey interactions between fishes and invertebrates within these systems over time may help elucidate predominant effects of macrophyte extirpation and seasonally abundant algae habitat on the food habits of fishes.

I examined the diet patterns of four species of fishes, *Lepomis punctatus*, *Micropterus salmoides*, *Lagodon rhomboides*, and *Lutjanus griseus,* within the Chassahowitzka and Homosassa rivers to evaluate the spatial and temporal heterogeneity in prey composition, selection, and foraging success associated with large-scale changes in vegetative habitat and prey availability. These species were selected because they represent a spectrum of functional feeding guilds and were common in both rivers during the period of study. I compared diet information between a highly vegetated river, the Chassahowitzka River, and one where macrophytes have been largely absent since 2006, the Homosassa River. I evaluated a combination of diet indices (Chipps and Garvey 2007) to evaluate (1) differences in prey composition between rivers and seasons, (2) prey selectivity of each species, and (3) predator relative foraging success in each river. By coupling quantitative estimates of aquatic vegetation and prey biomasses (Chapter 3) with information on the food habits of fishes, I provide an assessment of community structure necessary to evaluate combined bottom-up and top-down effects of altered vegetation composition and biomass on fish and invertebrate populations in coastal aquatic ecosystems.

Methods

Diet Sampling and Laboratory Procedures

The diet contents of *L. punctatus, M. salmoides, L. rhomboides*, and *L. griseus* were sampled using a nonlethal stomach flushing method (Kamler and Pope 2001) for individuals greater than or equal to 150 mm in total length, and by sacrificing individuals less than 150 mm in total length for diet analysis by dissection. Diet sampling was conducted in conjunction with electrofishing sampling for large-bodied fishes (Chapter 3); sampling occurred during January and July of years one and two, and monthly during year three. The gastric lavage apparatus used to flush stomachs comprised 1.2 m of 9.5-mm vinyl tubing attached to a 1,900- or 2,800-liter-per-minute bilge pump at one end, and a pistol grip, plastic hose nozzle at the opposite end. Vinyl tubing (3.1 mm diameter) was attached to the output of the nozzle for insertion through the esophagus of the fish. The bilge pump was anchored to the bottom of a 19-L plastic bucket and connected to a 12-V marine cell battery with a switch installed on the cathode wire. The bucket was filled with freshwater so that the pump generated a steady stream of water when the switch was turned on and the trigger was compressed. The 3.1-mm vinyl tubing was inserted into a fish’s esophagus, its stomach was filled with water, and the stomach contents were flushed into a plastic funnel by holding the fish mouth-down and pressing its stomach inward until the fish extruded the water and gut contents. The plastic collection funnel had a rubber stopper inserted into the bottom to prevent items from washing through, with holes drilled into the lower half of the funnel and covered with a 300-µm filter mesh fabric to allow water drainage but prevent the loss of prey items larger than 300 μm. The samples were washed from the funnel into a sealable plastic bag by pulling the rubber stopper and rinsing the inside of the funnel. Each sample was labeled with a unique diet identification number. Samples were transported on ice to the laboratory and frozen until processed.

In the laboratory, diet samples were thawed, and then rinsed into a 300-μm sieve. The contents were removed from the sieve and placed in a petri dish for examination under a stereo-dissecting microscope with magnification to 43x. For sacrificed fish, the stomach was removed and the contents were emptied into a petri dish for examination under the dissecting scope. Individual diet items were identified to the lowest possible taxonomic unit, dried in an oven at 70°C for a period of 24 h and then weighed at room temperature. When individual diet items could not be separated effectively, I recorded the approximate percent composition of each diet item along with the combined weight of all items. I then multiplied the percent composition by total diet weight to approximate the individual weight of each diet item.

Filamentous algae, detritus, plant material, and sediment were excluded from diet indices of *L. punctatus*, *M. salmoides*, and *L. griseus;* however, these prey groups were encountered frequently in mouths (*M. salmoides* particularly) and stomach samples. Detritus and sediment were excluded from the analysis of *L. rhomboides*; however, filamentous algae and plants were included in the diet indices since this species has been shown to be omnivorous in vegetated habitats (Montgomery and Targett 1992). Several invertebrate and fish taxa were combined into prey groups, including invertebrates associated with vegetation, benthic invertebrates, freshwater small-bodied fishes, saltwater small-bodied fishes, terrestrial invertebrates and terrestrial vertebrates. Vegetation associated invertebrates comprised copepods, gastropods, insect pupae/larvae, isopods, and tanaids. Benthic invertebrates comprised bivalves, nematodes, oligochaetes, ostracods, and polychaetes. Several invertebrate taxa were collected in both benthic and vegetative habitats (e.g., copepods, nematodes, ostracods, insect larvae); these taxa were grouped by habitat in which they were observed in greater abundance. Freshwater small-bodied fishes comprised *Fundulus* spp., *Gambusia* sp., *Lucania* spp., *Menidia* sp., *Notropis* spp., and *Poecilia* sp. Saltwater small-bodied fishes comprised *Anchoa* sp., *Brevoortia* sp., *Eucinostomus* spp., *Gobiosoma* sp., *Microgobius* sp., *Strongylura* spp., and *Trinectes* sp. Terrestrial invertebrates comprised arachnids, coleopterans, diplopodans, hymenopterans, lepidopterans, and orthopterans. Terrestrial vertebrates comprised bullfrogs, lizards, snakes, and juvenile waterfowl (observed in *Micropterus salmoides* within the Homosassa River).

Prey Composition Indices

The prey composition of each fish species was estimated for the Chassahowitzka and Homosassa rivers during summer months (June, July, and August) and winter months (December, January, and February) using mean proportion by dry weight and frequency of occurrence indices (Chipps and Garvey 2007). Diet samples were pooled across years to estimate mean proportion by river and season. The mean proportion by dry weight (MW_i) provided an estimate of the relative importance of each prey group to the predator, and was calculated as:

$$MW_i = \frac{1}{P}\sum_{j=1}^{P}\left(\frac{W_{ij}}{\sum_{i=1}^{Q} W_{ij}}\right) \tag{4-1}$$

where:
P = number of fish with food in their stomachs,
i = prey type,
j = fish stomach sample,
W = dry weight of prey item,
Q = total number of prey types

The mean frequency of occurrence (O_i) provided an estimate of how often individual prey groups were observed in fish diets, and was estimated as:

$$O_i = \frac{J_i}{P_i} \tag{4-2}$$

where:
i = prey type,
J = number of fish containing prey i
P = number of fish with food in their stomachs

I used a repeated measures multivariate analysis of variance (with Wilk's lambda as the test statistic) (Zar 1999) to test for significant differences in prey composition, measured as proportion by dry weight, between rivers and between seasons by river for each fish species. Significance level was 0.05 for all analysis of variance tests. In these analyses, the proportion by dry weight of each prey group was the response variable, individual fish were treated as replicates (pooled across years), and river or river*season was the treatment variable(s). I then conducted an analysis of variance for individual prey groups to assess which groups were significantly different between the rivers and seasons.

Prey Selectivity Indices

To examine predator preference for individual prey groups within each river, I calculated prey selectivity indices (Manly et al. 1972, Chesson 1983) using empirical estimates of average prey group biomass (Table 3-1) and mean prey proportion by dry weight in diets. Prey selectivity indices (α_i) were calculated separately by river and season (winter and summer) to assess how production of filamentous algae during winter affected the prey selection of predators. Prior to calculating the selectivity indices, estimates of prey biomass and mean proportion by dry weight were normalized across all prey groups for each season and river. Prey selectivity indices were calculated as:

$$\alpha_i = \frac{MW_i}{B_i}\left(\frac{1}{\sum_{i=1}^{Q}\left(MW_i/B_i\right)}\right) \tag{4-3}$$

where:
MW_i = mean proportion by dry weight of prey group i
B_i = estimated biomass of prey group i
Q = total number of prey groups i

Predator foraging was assumed to be nonselective when $\alpha_i = 1/Q$ across prey groups. Values of $\alpha_i > 1/Q$ indicated preference for that prey group (mean proportion in diet > proportion of estimated prey biomass), and values of $\alpha_i < 1/Q$ indicated avoidance (mean proportion in diet < proportion of estimated prey biomass).

Relative Foraging Success

To examine spatial and temporal patterns in predator foraging success, I calculated the proportion of empty stomachs (i.e. how many fish sampled contained prey) and the mean total prey dry weight per predator body weight. These metrics were calculated for individual sampling events to assess seasonal (years one, two, and three), interannual (years one, two, and three) and intra-annual (year three) patterns in stomach emptiness and relative prey consumption within each river, and to compare spatially between the rivers. The proportion of empty stomachs (E_j) was calculated as:

$$E_j = 1 - \frac{P_j}{N_j} \tag{4-4}$$

where:
P_j = Number of fish of predator j containing prey
N_j = Total number of fish sampled of predator j

The mean prey dry weight per predator body weight (MBW_j) provided a relative measure of the amount of prey consumed per predator, and was calculated as:

$$MBW_j = \frac{1}{P}\sum_{j=1}^{P}\left(\frac{W_j}{B_j}\right) \tag{4-5}$$

where:
P = number of fish with food in their stomachs,
j = fish stomach sample,
W = total dry weight of all prey items,
B = predator body weight

Predator body weight was calculated from measurements of predator total length and length-weight regression parameters from empirical length and weight data collected from the Chassahowitzka and Homosassa rivers (Lauretta, unpublished data). The estimates of proportion of empty stomachs and mean prey dry weight per predator body weight were plotted to visually compare between rivers and across sampling events. I used these comparisons to test whether predator foraging success is lower in the Homosassa River compared to the Chassahowitzka River.

Results

A total of 1,115 diet samples of *L. punctatus*, 1,155 diet samples of *M. salmoides*, 863 diet samples of *L. rhomboides*, and 863 diet samples of *L. griseus* were collected from the Chassahowitzka River between July 2007 and June 2010. A total of 411 diet samples of *L. punctatus*, 705 diet samples of *M. salmoides*, 393 diet samples of *L. rhomboides*, and 699 diet samples of *L. griseus* were collected from the Homosassa River during that period. Many diet samples contained unidentifiable prey items, on average about one out of every ten diets across species, with approximately five percent of the prey mass measured being indistinguishable between invertebrate or fish prey, on average. Over half of the diet samples of *M. salmoides* contained unidentifiable fishes. Invertebrates were more commonly identified by their hard parts and less error was associated with diet determination of *L. punctatus, L. rhomboides*, and *L. griseus*. As unidentified prey items may cause bias in the prey composition and selectivity indices, unidentified crustaceans, total crustaceans, unidentified invertebrates, total invertebrates, unidentified fish, and total fish prey were included as distinct categories in the diet composition indices. In addition, I calculated selectivity indices for freshwater and saltwater invertebrates and fishes separately. The bias from unidentified items is least for the coarsest resolution index (total fishes vs. total invertebrates) since I was able to effectively incorporate unidentified groups as either invertebrate or fish prey taxa. Results for individual species follow.

Lepomis punctatus

Prey composition

Diets of *L. punctatus* from the Chassahowitzka River contained a high proportion of amphipods, followed by vegetation associated invertebrates (Table 4-1). Samples from the Homosassa River contained a lower proportion of amphipods in comparison, especially during summer months (Table 4-1). Mud crabs (Grapsidae and Xanthidae) and terrestrial invertebrates were consumed in greater proportion during summer in the Homosassa River (Table 4-1) when vegetation and invertebrate biomass was lower. Overall, aquatic invertebrates comprised 80 to 90% of prey taxa for *L. punctatus* in both rivers, followed by terrestrial invertebrates and small-bodied fishes.

Multivariate analysis of variance indicated significantly different diet compositions between rivers ($p<0.001$). Analysis of variance by individual prey groups indicated that mean proportion by dry weight was significantly different between rivers for Amphipoda ($p<0.001$), Cambaridae (p-value=0.02), Grapsidae/Xanthidae ($p<0.001$), vegetation associated invertebrates ($p<0.001$), benthic invertebrates ($p<0.001$), and terrestrial invertebrates (p-value=0.006); and not significantly different for *Callinectes sapidus* (p-value=0.45) or *Palaemonetes* spp. (p-value=0.92).

Multivariate analysis of variance indicated significant differences in the seasonal diet composition of *L. punctatus* in the Chassahowitzka River ($p<0.001$) and the Homosassa River ($p<0.001$). Analysis of variance on individual prey groups indicated that Amphipoda ($p<0.001$), *Palaemonetes* spp. (p-value=0.04), Cambaridae (p-value=0.03), and terrestrial invertebrate ($p<0.001$) mean proportion by dry weight differed between seasons in the Chassahowitzka River; no significant differences in mean proportion by dry weight were detected between seasons for Grapsidae/Xanthidae (p-value=0.24), *Callinectes sapidus* (p-value=0.54), vegetation associated invertebrates (p-value=0.10), or benthic invertebrates (p-value=0.17). In the Homosassa River, mean proportion by dry weight differed significantly between seasons for Amphipoda (p<0.001), Grapsidae/Xanthidae (p<0.001), and terrestrial invertebrates (p<0.001). No significant difference between seasons was indicated for *Palaemonetes* spp. (p = 0.61), Cambaridae (p-value=0.48), *Callinectes sapidus* (p-value=0.37), vegetation associated invertebrates (p-value=0.63), or benthic invertebrates (p-value=0.20).

Amphipods were present in 80 to 90% of *L. punctatus* samples within the Chassahowitzka River during summer and winter. Diets of *L. punctatus* from the Homosassa River during summer had a lower frequency of occurrence of amphipods (34%) compared to winter (71%). Vegetation associated invertebrates were also commonly encountered in both rivers and during both sampling seasons (Table 4-2). Other common taxa observed during summer included terrestrial invertebrates in the Chassahowitzka River, and Grapsidae/Xanthidae, benthic invertebrates, and terrestrial invertebrates in the Homosassa River (Table 4-2).

Prey selectivity

Manly-Chesson indices indicated that *L. punctatus* selectively foraged on freshwater invertebrates in the Chassahowitzka River, particularly Amphipoda and other invertebrates associated with vegetation during both the summer and winter months (Table 4-3). *Lepomis punctatus* in the Homosassa River also selectively foraged on invertebrates, with distinct differences between seasons (Table 4-3). During summer, fish in the Chassahowitzka River selected for benthic invertebrates and those associated with vegetation, and during winter fish selected for Amphipoda and *Palaemonetes* spp. Fish in the Homosassa River selectively foraged on saltwater invertebrates in addition to freshwater invertebrates during summer months.

Relative foraging success

The majority of *L. punctatus* diets from both rivers contained prey, with <0.05 proportion of empty stomachs observed for most sampling events. The proportion of empty stomachs from the Homosassa River was equal to or less than the proportion from the Chassahowitzka River for all sample periods with the exception of the December 2009 and January 2010 (Figures 4-2 and 4-3). Mean total prey dry weight per predator body weight indices for *L. punctatus* in the Homosassa River were equal to or greater than indices from the Chassahowitzka River across all sample events with the exception of February 2010 and March 2010 sample periods (Figures 4-4 and 4-5). A seasonal increase in mean prey dry mass per predator body weight was observed during late spring and early summer in both rivers (Figure 4-5), with a higher mean observed in the Homosassa River during summer periods compared to winter (Figures 4-4 and 4-5).

Micropterus salmoides

Prey composition

Diets of *M. salmoides* from the Chassahowitzka River during summer contained a high proportion of Cambaridae, freshwater small-bodied fishes, and unidentified fish (Table 4-4). Winter sampling indicated a higher composition of Amphipoda, saltwater small-bodied fishes and *Palaemonetes* spp., and lower proportion of Cambaridae and freshwater small-bodied fishes, compared to summer. Samples from the Homosassa River contained a lower proportion of Cambaridae, particularly during summer months; a higher proportion of Grapsidae/Xanthidae, *Palaemonetes* spp., and saltwater small-bodied fishes; and an overall higher proportion of fish during both seasons (Table 4-4).

Multivariate analysis of variance indicated significantly different diet compositions between rivers (p<0.001). Analysis of variance of individual prey groups indicated that mean proportion by dry weight was significantly different between rivers for Amphipoda, (p-value=0.002), *Palaemonetes* spp. (p<0.001), Cambaridae (p<0.001), Grapsidae/Xanthidae (p<0.001), vegetation associated invertebrates (p<0.001), saltwater small-bodied fishes (p<0.001), and juvenile *Micropterus salmoides* (p-value=0.03). No significant difference in mean proportion by dry mass was detected for *Callinectes sapidus* (p-value=0.34), benthic invertebrates (p-value=0.28), freshwater small-bodied fishes (p-value=0.76), *Lepomis* spp. (p-value=0.48), *Erimyzon sucetta* (p-value=0.39), *Lagodon rhomboides* (p-value=0.25), *Lutjanus griseus* (p-value=0.34), terrestrial invertebrates (p-value=0.92), or terrestrial vertebrates (p-value=0.42).

Multivariate analysis of variance indicated significant differences in the seasonal diet composition of *M. salmoides* in the Chassahowitzka River (p<0.001) and the Homosassa River (p-value=0.002). Analysis of variance on individual prey groups indicated that Amphipoda (p<0.001), *Palaemonetes* spp. (p-value=0.001), Cambaridae (p<0.001), *Callinectes sapidus* (p-value=0.05), freshwater small-bodied fishes (p-value=0.006), saltwater small-bodied fishes (p<0.001), *Lutjanus griseus* (p-value=0.01) and terrestrial vertebrates (p-value=0.04) proportion by dry weight differed between seasons in the Chassahowitzka River. No significant differences in mean proportion by dry weight were detected between seasons for Grapsidae/Xanthidae (p-value=0.48), vegetation associated invertebrates (p-value=0.22), benthic invertebrates (p-value=0.42), *Lepomis* spp. (p-value=0.63), *Erimyzon sucetta* (p-value=0.21), juvenile *Micropterus salmoides* (p-value=0.43), *Lagodon rhomboides* (p-value=0.26), *Mugil* *cephalus* (p-value=0.43), *Archosargus probatocephalus* (p-value=0.21), and terrestrial invertebrates (p-value=0.23). In the Homosassa River, mean proportion by dry weight differed significantly between seasons for Amphipoda (p<0.001) and saltwater small-bodied fishes (p-value=0.04). No significant difference between seasons was indicated for *Palaemonetes* spp. (p = 0.35), Cambaridae (p-value=0.11), Grapsidae/Xanthidae (p-value=0.21), *Callinectes sapidus* (p-value=0.,08), vegetation associated invertebrates (p-value=0.37), benthic invertebrates (p-value=0.39), freshwater small-bodied fishes (p-value=0.34), *Lepomis* spp. (p-value=0.91), juvenile *Micropterus salmoides* (p-value=0.71), *Lagodon rhomboides* (p-value=0.55), *Archosargus probatocephalus* (p-value=0.52), *Lutjanus griseus* (p-value=0.12), terrestrial invertebrates (p-value=0.33), or terrestrial vertebrates (p-value=0.30).

Unidentified fish remains were the most common diet item encountered in *M. salmoides* diets in the Chassahowitzka and Homosassa rivers during both seasons. The highest frequency of occurrence of identified prey groups in the Chassahowitzka River was observed for Cambaridae, freshwater small-bodied fishes, vegetation associated invertebrates, and Amphipoda during summer months; and Amphipoda, freshwater small-bodied fishes, Cambaridae, saltwater small-bodied fishes, and *Palaemonetes* spp. during winter months (Table 4-5). In the Homosassa River during summer, freshwater small-bodied fishes, *Palaemonetes* spp., saltwater small-bodied fishes and Cambaridae were the most commonly encountered identifiable prey groups (Table 4-5). During winter, Amphipoda had the highest frequency of occurrence, followed by freshwater small-bodied fishes, saltwater small-bodied fishes, and

Palaemonetes spp., all of which occurred in at least one out of every ten diet samples (Table 4-5).

Prey selectivity

Manly-Chesson indices indicated that *M. salmoides* selectively foraged on freshwater small-bodied fishes across both seasons and in both rivers (Table 4-6). *Micropterus salmoides* also selectively cannibalized juveniles during summer months in both rivers. Other prey groups that were selected for during summer included Cambaridae, *L. rhomboides*, vegetation associated invertebrates, and Amphipoda in the Chassahowitzka River; and *Lepomis* spp. and vegetation associated invertebrates in the Homosassa River. Overall, *M. salmoides* selectively foraged on fishes, especially freshwater fishes, during summer in the Chassahowitzka and winter in both rivers. Selection was greater for invertebrates (freshwater taxa) during summer months in the Homosassa River.

Relative foraging success

The proportion of empty stomachs increased during winter months in the Chassahowitzka River, but this pattern was not apparent across years in the Homosassa River (Figures 4-2 and 4-3). A seasonal pattern in mean total prey dry weight per predator body weight was observed in the Homosassa River; means were higher during summer months compared to winter (Figures 4-4 and 4-5). This pattern was not apparent in the Chassahowitzka River. Overall, I did not observe a higher proportion of empty stomachs or lower mean total prey dry mass per predator body weight in the Homosassa River, despite lower prey biomass (Cambaridae and freshwater small-bodied fishes, in particular).

Lagodon rhomboides

Prey composition

Diets of *L. rhomboides* from the Chassahowitzka and Homosassa rivers during summer and winter contained mostly filamentous algae, Amphipoda, and vegetation associated invertebrates (Table 4-7). Diets taken during winter from the Homosassa River contained a higher proportion of Amphipoda compared to summer months (Table 4-7).

Multivariate analysis of variance indicated significantly different diet compositions between rivers ($p<0.001$). Analysis of variance of individual prey groups indicated that mean proportion by dry weight was significantly different between rivers for filamentous algae, ($p<0.001$), macrophytes ($p<0.001$), Cambaridae (p-value=0.006), Grapsidae/Xanthidae ($p<0.001$), and benthic invertebrates (p-value=0.05). No significant difference in mean proportion by dry mass was detected for Amphipoda (p-value=0.49), *Palaemonetes* spp. (p-value=0.25), *Callinectes sapidus* (p-value=0.10), vegetation associated invertebrates (p-value=0.76), saltwater small-bodied fishes (p-value=0.49), or terrestrial invertebrates (p-value=0.34).

Multivariate analysis of variance indicated significant differences in the seasonal diet composition of *L. rhomboides* in the Chassahowitzka River ($p<0.001$) and the Homosassa River ($p<0.001$). Analysis of variance on individual prey groups indicated that macrophytes ($p<0.001$), Amphipoda (p-value=0.02), *Palaemonetes* spp. (p-value=0.007), Cambaridae (p-value=0.005), and benthic invertebrates (p-value=0.05) proportion by dry weight differed between seasons in the Chassahowitzka River; no significant differences in mean proportion by dry weight were detected between seasons for filamentous algae (p-value=0.08), *Callinectes sapidus* (p-value=0.15), vegetation associated invertebrates (p-value=0.77), saltwater small-bodied fishes (p-value=0.47), or terrestrial invertebrates (p-value=0.23). In the Homosassa River, mean proportion by dry weight differed significantly between seasons for filamentous algae ($p<0.001$), Amphipoda ($p<0.001$), and Grapsidae/Xanthidae (p-value=0.01). No significant difference between seasons was indicated for macrophytes (p-value=0.73), *Palaemonetes* spp. ($p = 0.36$), Cambaridae (p-value=0.41), vegetation associated invertebrates (p-value=0.23), benthic invertebrates (p-value=0.07), or terrestrial invertebrates (p-value=0.56).

The most frequently identified prey groups of *L. rhomboides* in the Chassahowitzka River were filamentous algae, Amphipoda, and vegetation associated invertebrates during both summer and winter (Table 4-8). In the Homosassa River, filamentous algae and amphipods were also commonly encountered in diets; however, the frequency of Amphipoda in the diets was more than double during winter than during summer (Table 4-8).

Prey selectivity

Manly-Chesson indices indicated that *L. rhomboides* selectively foraged on Amphipoda and benthic invertebrates in both rivers during summer and winter (Table 4-9). Fish also selected for vegetation associated invertebrates during winter in the Chassahowitzka River and summer in the Homosassa River.

Relative foraging success

Lagodon rhomboides diets were rarely empty, as a result of a high proportion of diets containing filamentous algae and the inclusion of this prey group in the diet indices. Overall, I did not observe a higher proportion of empty stomachs in the Chassahowitzka River during any sampling event with the exception of November 2009

(Figures 4-2 and 4-3). Mean total prey dry weight per predator body weight was less variable in the Chassahowitzka River compared to the Homosassa River, with a seasonally higher mean in the Homosassa River during summer months (Figures 4-4 and 4-5). In general, mean total prey dry mass per predator body weight was greater in the Homosassa River for most sampling events with the exception of January 2009 and January 2010.

Lutjanus griseus

Prey composition

Diets of *L. griseus* from the Chassahowitzka and Homosassa rivers during summer contained approximately half fishes and half invertebrates with a large proportion of unidentified fish; samples from winter contained greater than 75% invertebrates, mostly crustaceans (Table 4-10). *L. griseus* consumed a range of crustaceans, freshwater fishes, and saltwater fishes during summer in both rivers. In winter, mean prey proportion by dry weight was greatest for Amphipoda in the Chassahowitzka River, and Grapsidae/Xanthidae and Amphipoda in the Homosassa River.

Multivariate analysis of variance indicated significantly different diet compositions between rivers ($p<0.001$). Analysis of variance of individual prey groups indicated that mean proportion by dry weight was significantly different between rivers for Amphipoda, ($p<.001$), Cambaridae ($p<0.001$), Grapsidae/Xanthidae ($p<0.001$), and vegetation associated invertebrates (p-value=0.01). No significant difference in mean proportion by dry mass was detected for *Palaemonetes* spp. (p-value=0.07), *Callinectes sapidus* (p-value=0.99), benthic invertebrates (p-value=0.92), freshwater small-bodied fishes (p-value=0.60), *Lepomis* spp. (p-value=0.86), saltwater small-bodied fishes (p-value=0.06), *Lagodon rhomboides* (p-value=0.20), or terrestrial invertebrates (p-value=0.36).

Multivariate analysis of variance indicated significant differences in the seasonal diet composition of *L. griseus* in the Chassahowitzka River (p<0.001) and the Homosassa River (p<0.001). Analysis of variance on individual prey groups indicated that Amphipoda (p<0.001), *Palaemonetes* spp. (p-value=0.02), vegetation associated invertebrates (p-value=0.04), freshwater small-bodied fishes (p<0.001), *Lepomis* spp. (p-value=0.007), and *L. rhomboides* (p-value=0.03) proportion by dry weight differed between seasons in the Chassahowitzka River. No significant differences in mean proportion by dry weight were detected between seasons for Cambaridae (p-value=0.83), Grapsidae/Xanthidae (p-value=0.37), *Callinectes sapidus* (p-value=0.27), benthic invertebrates (p-value=0.13), saltwater small-bodied fishes (p-value=0.24), or terrestrial invertebrates (p-value=0.71). In the Homosassa River, mean proportion by dry weight differed significantly between seasons for Amphipoda (p<0.001), *Palaemonetes* spp. (p-value=0.01), and freshwater small-bodied fishes (p-value=0.05). No significant difference between seasons was indicated for Cambaridae (p-value=0.08), Grapsidae/Xanthidae (p-value=0.32), *Callinectes sapidus* (p-value=0.85), vegetation associated invertebrates (p-value=0.91), benthic invertebrates (p-value=0.53), *Lepomis* spp. (p-value=0.10), or saltwater small-bodied fishes (p-value=0.50).

Unidentified fish remains were the most common diet item encountered in *L. griseus* diets in the Chassahowitzka and Homosassa rivers during summer. The highest frequency of occurrence of identified prey groups in the Chassahowitzka River was observed for Amphipoda, unidentified crustacean, freshwater small-bodied fishes, *Palaemonetes* spp., Grapsidae/Xanthidae, Cambaridae, and vegetation associated invertebrates during summer months; and Amphipoda, vegetation associated invertebrates, Cambaridae and Grapsidae/Xanthidae during winter months (Table 4-11). In the Homosassa River during summer, freshwater small-bodied fishes, Grapsidae/Xanthidae, *Palaemonetes* spp., and vegetation associated invertebrates were the most commonly encountered identifiable prey groups (Table 4-11). During winter, the highest frequency of occurrence was observed for Amphipoda and Grapsidae/Xanthidae, followed by vegetation associated invertebrates and *Palaemonetes* spp. (Table 4-11).

Prey selectivity

Manly-Chesson indices indicated that *L. griseus* selectively foraged on Grapsidae/Xanthidae, Amphipoda, *L. rhomboides*, freshwater small-bodied fishes and *Palaemonetes* spp. during summer in the Chassahowitzka River (Table 4-12). During winter, *L. griseus* selectively foraged on Grapsidae/Xanthidae and freshwater small-bodied fishes. *Lutjanus griseus* in the Homosassa River selected for Grapsidae/Xanthidae during summer months, and *Palaemonetes* spp., freshwater small-bodied fishes, and Amphipoda during winter. Overall, *L. griseus* selectively foraged on fishes in the Chassahowitzka River during summer and freshwater invertebrates during winter. Selection was greatest for saltwater invertebrates (mainly Grapsidae/Xanthidae) during summer months in the Homosassa River, and freshwater invertebrates, saltwater invertebrates, and freshwater fishes during winter months.

Relative foraging success

The proportion of empty stomachs was not higher in the Homosassa River compared to the Chassahowitzka River across most sampling periods (Figure 4-2), although a seasonal increase in the proportion was observed during November, December, and January in the Homosassa River (Figure 4-3) when the density of *L. griseus* increased greatly as fish migrated into the rivers from the Gulf of Mexico (Figure 3-18). No seasonal pattern in mean total prey dry weight per predator body weight was detected across years in either river (Figure 4-4), but an increase in the mean was observed during late spring in 2010 (Figure 4-5) when filamentous algae production was high in both rivers (Figure 4-1). Overall, I did not observe a higher proportion of empty stomachs or lower mean total prey dry mass per predator body weight in the Homosassa River compared to the Chassahowitzka River.

Discussion

Vegetative habitat in coastal rivers influences the prey composition, selection, and relative consumption of fishes through bottom-up controls on crustaceans and other invertebrate prey, and by mediating top-down controls by freshwater and marine predators on prey populations. I found that aquatic vegetation composition and biomass influenced the prey composition, selectivity and consumption of fishes in coastal rivers by providing a primary food source and refuge habitat for high nutritional quality prey populations, including freshwater small-bodied fishes, Amphipoda, Cambaridae, and other invertebrate taxa. Specifically, I documented that diet composition was significantly different between rivers with different vegetation communities and between seasons with different prey communities for all four predator species assessed. I also documented that predatory fish were selectively feeding on prey resources in both rivers despite differences in habitat and prey availability and that that predator foraging success in a river where macrophytes are largely absent (Homosassa River) is equal to or greater than foraging success in a river with high macrophyte biomass (Chassahowitzka River). Combined, these results suggest that the loss of macrophytes and associated decline in associated prey populations likely results in prey switching by predators to taxa associated with alternative habitats such as Amphipoda (filamentous algae habitat), Grapsidae/Xanthidae (benthic substrates and filamentous algae habitats), and saltwater small-bodied fishes (pelagic and demersal habitats) depending on the seasonal production of filamentous algae and availability of saltwater prey species. This switching behavior may allow for the persistence of prey populations in coastal rivers (Comins and Hassel 1975, Baalen et al. 2001), despite low habitat availability (and likely increased predation risk) and decreased population densities.

As native macrophytes have declined in the Homosassa River, the role of filamentous algae in providing predation refuge is likely key in structuring predator-prey dynamics. Production of filamentous algae creates temporary habitat patches that are rapidly colonized by invertebrates, including Amphipoda and vegetation associated invertebrates. These dense vegetated habitats may inhibit predator foraging and provide abundant food resources (algae and associated periphyton, including diatoms) for grazing invertebrates allowing prey population densities to increase greatly in filamentous algae patches. This is evidenced by observed seasonal increases in density and biomass of these prey taxa during periods of high algae production, despite increased density of predators in the river, particularly *L. griseus* (Chapter 3).

Furthermore, predator foraging success was lower during winter in both rivers despite higher biomass of preferred prey groups, perhaps as a result of interference among predators at high densities, or decreased vulnerability of prey populations in a highly structured and productive habitat (Camp 2010, Camp et al. 2011). Alternatively, predation of small-bodied fishes by migratory predators (*L. griseus*, in particular) and subsequent population declines in fall through winter each year may have resulted in decreased predation pressure on invertebrates in vegetative habitats, since small-bodied fish predation on invertebrates is less likely to be inhibited by aquatic vegetation compared to larger-bodied fishes.

Fishes in the Chassahowitzka River foraged on a significantly higher proportion of Amphipoda (*L. punctatus* and *L. griseus*) and Cambaridae (*M. salmoides* and *L. griseus*), especially during summer months, compared to the Homosassa River where fishes consumed a significantly higher proportion of Grapsidae/Xanthidae (*L. punctatus*, *L. rhomboides* and *L. griseus*), *Palaemonetes* spp. (*M. salmoides*) and saltwater small-bodied fishes (*M. salmoides*). Interestingly, I did not detect a difference in the proportion of freshwater small-bodied fishes in diets between rivers, despite large differences in the estimated biomass of this prey group in each river (Chapter 3). Similarly, the proportion of vegetation associated invertebrates and *Palaemonetes* spp. in diets was not lower in fishes from the Homosassa River (proportion of *Palaemonetes* spp. was higher in *M. salmoides* diets), despite the disparity in macrophyte habitat. Based on these results, I infer that macrophyte habitat loss affects the prey composition of freshwater and saltwater fishes in coastal rivers through decreased availability and consumption of select phytophilic crustaceans, primarily Amphipoda and Cambaridae.

Frequency of occurrence indices confirmed seasonal differences in prey items for all predator species examined. Fishes in the Chassahowitzka River foraged on a significantly higher proportion of Cambaridae, *Palaemonetes* spp., and freshwater small-bodied fishes during summer months. Fishes in the Homosassa River consumed a significantly higher proportion of Grapsidae/Xanthidae, *Palaemonetes* spp., freshwater small-bodied fishes and terrestrial prey during summer months. A significantly higher proportion of Amphipoda and saltwater small-bodied fishes was observed in diets from the Chassahowitzka and Homosassa rivers during winter months coincident with high production of filamentous algae and increased density of saltwater fishes. These results suggest that seasonal production of filamentous algae indirectly affects the prey composition of fishes in coastal rivers by providing increased habitat and food availability for select prey groups, especially Amphipoda. In addition, larger predators preyed upon a greater proportion of freshwater small-bodied fishes in the summer and saltwater small-bodied fishes in the winter, providing further evidence of prey switching to seasonally abundant prey resources.

I found that predators were selectively foraging on prey groups in each river, but that this selection differed between rivers. *L. punctatus* selected for Amphipoda and vegetation associated invertebrates during both seasons in the Chassahowitzka River, but only during winter in the Homosassa River. This is likely because this species selected for vegetative and benthic invertebrates in the Homosassa River during summer when filamentous algae and Amphipoda biomass were relatively low. I found that *M. salmoides* selectively foraged on freshwater small-bodied fishes and select crustaceans, with distinct differences in the type of crustaceans foraged on between rivers and seasons. Selection for some crustacean prey could not be quantified in the Homosassa River because these taxa were not captured during sampling efforts to quantify availability (a gear selectivity issue for Cambaridae and *Palaemonetes* spp.), although these taxa were observed in the predator diets, indicating high selectivity (prey consumed in high proportion at low biomass). *Lagodon rhomboides* selectivity indices indicated avoidance of filamentous algae and plants. This species selectively consumed Amphipoda, vegetation associated invertebrates and benthic invertebrates in both rivers. Similar to *M. salmoides*, *L. griseus* selectively foraged on freshwater small-bodied fishes and select crustaceans, with differences in prey selection between seasons and rivers. These results clearly show that diet selection of fishes in the coastal rivers was for prey items with high caloric value, mostly small fishes and crustaceans. Tetzlaff (2008) documented larger home ranges and daily movement patterns of *M. salmoides* in the Homosassa compared to Chassahowitzka River likely due to increased searching time when foraging, as a result of decreased prey availability. Tetzlaff et al. (2009) found higher *M. salmoides* prey consumption rates in the Homosassa River compared to the Chassahowitzka, likely driven by increased foraging activity in the Homosassa River, and increased prey vulnerability in an unstructured river.

I found that the proportion of empty predator stomachs was not lower in the Homosassa River for any of the predator species evaluated, nor was the average prey dry weight per predator body weight lower. In fact, the proportion of empty stomachs was lower, and the average prey dry weight per predator body weight was generally higher for each species in the Homosassa River. This suggests that predator foraging success in the Homosassa River is equal to or greater than foraging success in the Chassahowitzka River. This result is somewhat surprising given the large differences in prey biomass between rivers (Chapter 3) and is likely a result of the utilization of alternative prey groups, including saltwater invertebrates and fishes. However, there may be an increased energy cost associated with foraging in an open water environment compared to a vegetated one with higher prey density when prey encounters are less frequent (Savino and Stein 1989, Tetzlaff 2008, Tetzlaff et al. 2010).

Table 4-1. Mean proportion by dry weight of common prey taxa observed in stomachs of *Lepomis punctatus* from the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	390	379	145	119
Amphipoda	0.55	0.69	0.13	0.45
Palaemonetes spp.	0.02	0.01	0.02	0.01
Cambaridae	0.03	0.01	0.01	0.001
Grapsidae/Xanthidae	0.002	0.01	0.17	0.03
Callinectes sapidus	0.01	0.004	0.004	0
Unidentified crab	0.003	0.0004	0.05	0.02
Unidentified crustacean	0.01	0.01	0.03	0.01
Total crustaceans	0.63	0.73	0.41	0.53
Vegetative invertebrates	0.20	0.17	0.27	0.29
Benthic invertebrates	0.01	0.02	0.07	0.04
Unidentified invertebrates	0.03	0.01	0.05	0.03
Total invertebrates	0.87	0.93	0.79	0.89
Fish eggs	0.003	0.003	0.0004	0.001
Freshwater small-bodied fishes	0.002	0	0.003	0.004
Saltwater small-bodied fishes	0	0	0.003	0.01
Unidentified fish	0.03	0.01	0.04	0.02
Total fish	0.04	0.01	0.05	0.03
Terrestrial invertebrates	0.07	0.02	0.11	0.03
Terrestrial vertebrates	0	0	0.01	0.01
Unidentified prey	0.02	0.04	0.05	0.05

Table 4-2. Percent frequency of occurrence of common prey taxa observed in stomachs of *Lepomis punctatus* from the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	383	379	145	119
Amphipoda	82	91	34	71
Palaemonetes spp.	6	3	6	3
Cambaridae	6	3	1	1
Grapsidae/Xanthidae	1	2	25	6
Callinectes sapidus	1	1	1	0
Unidentified crab	1	1	8	4
Unidentified crustacean	3	2	6	3
Vegetative invertebrates	66	52	59	61
Benthic invertebrates	11	10	19	17
Unidentified invertebrates	7	4	12	5
Fish eggs	2	1	1	2
Freshwater small-bodied fishes	0.3	0	1	1
Saltwater small-bodied fishes	0	0	1	1
Unidentified fish	7	4	12	3
Terrestrial invertebrates	24	6	32	9
Terrestrial vertebrates	0	0	1	1
Unidentified prey	7	9	14	8

Table 4-3. Manly-Chesson prey selectivity indices for *Lepomis punctatus* from the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	317	331	128	114
Preference value (1/Q)	0.11	0.11	0.17	0.13
Amphipoda	0.71	0.35	0.07	0.34
Palaemonetes spp.	0.01	0.03	-	0.36
Cambaridae	0.00	0.03	-	-
Vegetative invertebrates	0.21	0.32	0.51	0.07
Benthic invertebrates	0.05	0.15	0.29	0.09
Callinectes sapidus	0.00	0.00	-	0.00
Grapsidae/Xanthidae	0.00	0.12	0.13	0.00
Freshwater small-bodied fishes	0.00	0.00	0.00	0.13
Saltwater small-bodied fishes	0.00	0.00	0.00	0.01
Freshwater invertebrates	0.92	0.98	0.58	0.71
Saltwater invertebrates	0.07	0.02	0.41	0.05
Freshwater fishes	0.01	0.00	0.00	0.22
Saltwater fishes	0.00	0.00	0.00	0.02
Total invertebrates	0.92	0.98	0.98	0.88
Total fishes	0.08	0.02	0.02	0.12

Table 4-4. Mean proportion by dry weight of common prey taxa observed in stomachs of *Micropterus salmoides* from the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	384	240	317	134
Amphipoda	0.02	0.08	0.01	0.05
Palaemonetes spp.	0.01	0.05	0.09	0.07
Cambaridae	0.23	0.09	0.07	0.03
Grapsidae/Xanthidae	0.002	0.0002	0.02	0.03
Callinectes sapidus	0.01	0	0.02	0.0002
Unidentified crab	0.0001	0	0.001	0.01
Unidentified crustacean	0.02	0.01	0.02	0.02
Total crustaceans	0.30	0.23	0.23	0.22
Vegetative invertebrates	0.04	0.06	0.02	0.01
Benthic invertebrates	0.01	0.003	0.002	0.0004
Unidentified invertebrates	0.02	0.003	0.01	0
Total invertebrates	0.37	0.29	0.26	0.22
Freshwater small-bodied fishes	0.20	0.12	0.18	0.15
Lepomis spp.	0.02	0.02	0.03	0.03
Erimyzon sucetta	0	0.003	0	0
Micropterus salmoides	0.002	0	0.01	0.01
Saltwater small-bodied fishes	0.01	0.07	0.06	0.12
Lagodon rhomboides	0.02	0.01	0.01	0.01
Archosargus probatocephalus	0	0.004	0.0002	0
Mugil cephalus	0.002	0	0	0
Lutjanus griseus	0	0.01	0	0.01
Unidentified fish	0.32	0.39	0.41	0.43
Total fish	0.57	0.64	0.70	0.75
Terrestrial invertebrates	0.003	0.01	0.01	0.0003
Terrestrial vertebrates	0.01	0	0.01	0
Unidentified prey	0.04	0.06	0.03	0.03

Table 4-5. Percent frequency of occurrence of common prey taxa observed in stomachs of *Micropterus salmoides* from the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	384	240	317	134
Amphipoda	12	27	5	22
Palaemonetes spp.	4	8	16	10
Cambaridae	27	13	9	4
Grapsidae/Xanthidae	0.3	0.4	4	6
Callinectes sapidus	2	0	3	1
Unidentified crab	0.3	0	1	3
Unidentified crustacean	5	3	6	6
Vegetative invertebrates	16	12	7	8
Benthic invertebrates	3	1	2	2
Unidentified invertebrates	5	0.4	3	0
Fish eggs	1	1	0	1
Freshwater small-bodied fishes	25	15	22	17
Lepomis spp.	2	3	4	4
Erimyzon sucetta	0	0.4	0	0
Micropterus salmoides	0.3	0	1	1
Saltwater small-bodied fishes	1	8	9	14
Lagodon rhomboides	2	1	1	1
Mugil cephalus	0.3	0	0	0
Archosargus probatocephalus	0	0.4	0.3	0
Lutjanus griseus	0	2	0	1
Unidentified fish	49	52	56	60
Terrestrial invertebrates	1	1	2	1
Terrestrial vertebrates	2	0	1	0
Unidentified prey	5	8	6	4

Table 4-6. Manly-Chesson prey selectivity indices for *Micropterus salmoides* from the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	329	202	269	116
Preference value (1/Q)	0.06	0.06	0.08	0.07
Amphipoda	0.07	0.00	0.01	0.00
Palaemonetes spp.	0.02	0.01	-	0.22
Cambaridae	0.08	0.02	-	-
Vegetative invertebrates	0.09	0.01	0.10	0.00
Benthic invertebrates	0.04	0.00	0.02	0.00
Callinectes sapidus	0.02	0.00	-	0.00
Grapsidae/Xanthidae	0.00	0.00	0.05	0.00
Freshwater small-bodied fishes	0.23	0.62	0.34	0.47
Erimyzon sucetta	0.00	0.01	0.00	-
Lepomis spp.	0.08	0.01	0.20	0.11
Micropterus salmoides	0.25	0.00	0.26	0.00
Saltwater small-bodied fishes	0.01	0.01	0.02	0.01
Mugil cephalus	0.02	0.00	0.00	0.00
Lagodon rhomboides	0.09	0.01	0.00	0.18
Archosargus probatocephalus	0.00	0.30	0.01	0.00
Lutjanus griseus	0.00	0.00	0.00	0.00
Freshwater invertebrates	0.23	0.14	0.46	0.01
Saltwater invertebrates	0.06	0.00	0.13	0.01
Freshwater fishes	0.64	0.75	0.38	0.94
Saltwater fishes	0.07	0.11	0.03	0.04
Total invertebrates	0.24	0.16	0.63	0.06
Total fishes	0.76	0.84	0.37	0.94

Table 4-7. Mean proportion by dry weight of common prey taxa observed in stomachs of *Lagodon rhomboides* from the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	434	207	184	64
Filamentous algae	0.63	0.70	0.56	0.32
Vascular plants	0.01	0.06	0.004	0.005
Amphipoda	0.17	0.10	0.12	0.42
Palaemonetes spp.	0.002	0.017	0.005	0
Cambaridae	0.03	0	0.001	0
Grapsidae/Xanthidae	0	0	0.07	0
Callinectes sapidus	0	0.001	0	0
Unidentified crab	0.01	0	0.05	0.01
Unidentified crustacean	0.01	0	0.01	0
Total crustaceans	0.21	0.12	0.26	0.44
Vegetative invertebrates	0.06	0.07	0.05	0.08
Benthic invertebrates	0.03	0.01	0.03	0.06
Unidentified invertebrates	0.002	0.01	0.02	0
Total invertebrates	0.31	0.21	0.35	0.57
Saltwater small-bodied fishes	0.001	0	0	0
Unidentified fish	0.01	0	0.06	0.01
Total fish	0.01	0.0002	0.06	0.01
Terrestrial invertebrates	0.002	0.006	0.0003	0
Unidentified prey	0.04	0.02	0.03	0.09

Table 4-8. Percent frequency of occurrence of common prey taxa observed in stomachs of *Lagodon rhomboides* from the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	429	207	184	64
Filamentous algae	84	86	78	59
Vascular plants	4	14	4	6
Amphipoda	34	25	30	70
Palaemonetes spp.	1	4	2	0
Cambaridae	5	0	1	0
Grapsidae/Xanthidae	0	0	11	0
Callinectes sapidus	0	0.5	0	0
Unidentified crab	1	0	7	2
Unidentified crustacean	4	0	5	0
Vegetative invertebrates	31	22	21	31
Benthic invertebrates	10	9	9	23
Unidentified invertebrates	3	2	4	0
Fish eggs	0	0.5	0	0
Freshwater small-bodied fishes	0.5	0	0	0
Saltwater small-bodied fishes	0.5	0	0	0
Unidentified fish	4	0	11	2
Terrestrial invertebrates	0.5	1	1	0
Unidentified prey	14	11	15	25

Table 4-9. Manly-Chesson prey selectivity indices for *Lagodon rhomboides* from the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	367	189	141	53
Preference value (1/Q)	0.13	0.13	0.17	0.14
Filamentous algae	0.07	0.05	0.02	0.02
Vascular plants	0.00	0.00	0.00	0.01
Amphipoda	0.53	0.15	0.20	0.68
Palaemonetes spp.	0.00	0.22	-	0.00
Cambaridae	0.01	0.00	-	-
Vegetative invertebrates	0.13	0.36	0.29	0.04
Benthic invertebrates	0.26	0.22	0.29	0.26
Grapsidae/Xanthidae	0.00	0.00	0.19	0.00
Filamentous algae	0.55	0.22	0.04	0.07
Vascular plants	0.00	0.01	0.00	0.05
Saltwater invertebrates	0.03	0.01	0.55	0.04
Freshwater invertebrates	0.43	0.77	0.41	0.85

Table 4-10. Mean proportion by dry weight of common prey taxa observed in stomachs of *Lutjanus griseus* from the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	64	423	102	217
Amphipoda	0.13	0.57	0.02	0.28
Palaemonetes spp.	0.06	0.02	0.09	0.04
Cambaridae	0.06	0.05	0.03	0.01
Grapsidae/Xanthidae	0.09	0.05	0.30	0.35
Callinectes sapidus	0.01	0.02	0.01	0.01
Unidentified crab	0.01	0.004	0.004	0.004
Unidentified crustacean	0.05	0.01	0.06	0.02
Total crustaceans	0.41	0.73	0.51	0.71
Vegetative invertebrates	0.01	0.06	0.02	0.02
Benthic invertebrates	0	0.02	0.02	0.03
Terrestrial invertebrates	0	0.002	0	0
Unidentified invertebrates	0.01	0.01	0.003	0.01
Total invertebrates	0.44	0.82	0.56	0.77
Freshwater small-bodied fishes	0.11	0.01	0.05	0.01
Lepomis spp.	0.02	0.00	0.01	0.00
Saltwater small-bodied fishes	0.03	0.01	0.02	0.03
Lagodon rhomboides	0.03	0.00	0.00	0.00
Unidentified fish	0.34	0.09	0.36	0.12
Total fish	0.52	0.12	0.44	0.17
Unidentified prey	0.04	0.06	0.01	0.06

Table 4-11. Percent frequency of occurrence of common prey taxa observed in stomachs of *Lutjanus griseus* from the Chassahowitzka and Homosassa rivers, Florida.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	58	423	102	217
Amphipoda	22	77	5	46
Palaemonetes spp.	14	5	20	7
Cambaridae	9	8	4	1
Grapsidae/Xanthidae	14	7	46	40
Callinectes sapidus	0	2	2	1
Unidentified crab	2	0.5	1	0.5
Unidentified crustacean	17	1	13	3
Vegetative invertebrates	10	23	13	13
Benthic invertebrates	0	7	6	9
Unidentified invertebrates	0	2	3	2
Fish eggs	0	0	1	0
Freshwater small-bodied fishes	16	3	7	2
Lepomis spp.	2	0	2	0
Saltwater small-bodied fishes	5	2	3	4
Lagodon rhomboides	3	0	0	0
Unidentified fish	52	17	54	17
Terrestrial invertebrates	0	0.2	0	0
Unidentified prey	3	12	3	9

Table 4-12. Manly-Chesson prey selectivity indices for *Lutjanus griseus* from the Chassahowitzka and Homosassa rivers, Florida. Spaces in the table separate the different prey grouping methods, which include identifiable taxa, saltwater and freshwater invertebrates and fishes, and invertebrates and fishes.

	Chassahowitzka River		Homosassa River	
	Summer	Winter	Summer	Winter
Sample size	53	358	81	194
Preference value (1/Q)	0.09	0.09	0.13	0.10
Amphipoda	0.18	0.08	0.02	0.11
Palaemonetes spp.	0.10	0.02	NA	0.56
Cambaridae	0.02	0.04	NA	NA
Vegetative invertebrates	0.04	0.04	0.12	0.00
Benthic invertebrates	0.00	0.04	0.03	0.03
Callinectes sapidus	0.00	0.00	NA	0.02
Grapsidae/Xanthidae	0.31	0.47	0.65	0.05
Freshwater small-bodied fishes	0.10	0.29	0.08	0.22
Lepomis spp.	0.06	0.00	0.09	0.00
Saltwater small-bodied fishes	0.02	0.01	0.00	0.01
Lagodon rhomboides	0.16	0.00	0.00	0.00
Freshwater invertebrates	0.17	0.67	0.25	0.21
Saltwater invertebrates	0.34	0.16	0.68	0.30
Freshwater fishes	0.33	0.14	0.07	0.44
Saltwater fishes	0.16	0.03	0.00	0.05
Total invertebrates	0.25	0.70	0.84	0.53
Total fishes	0.75	0.30	0.16	0.47

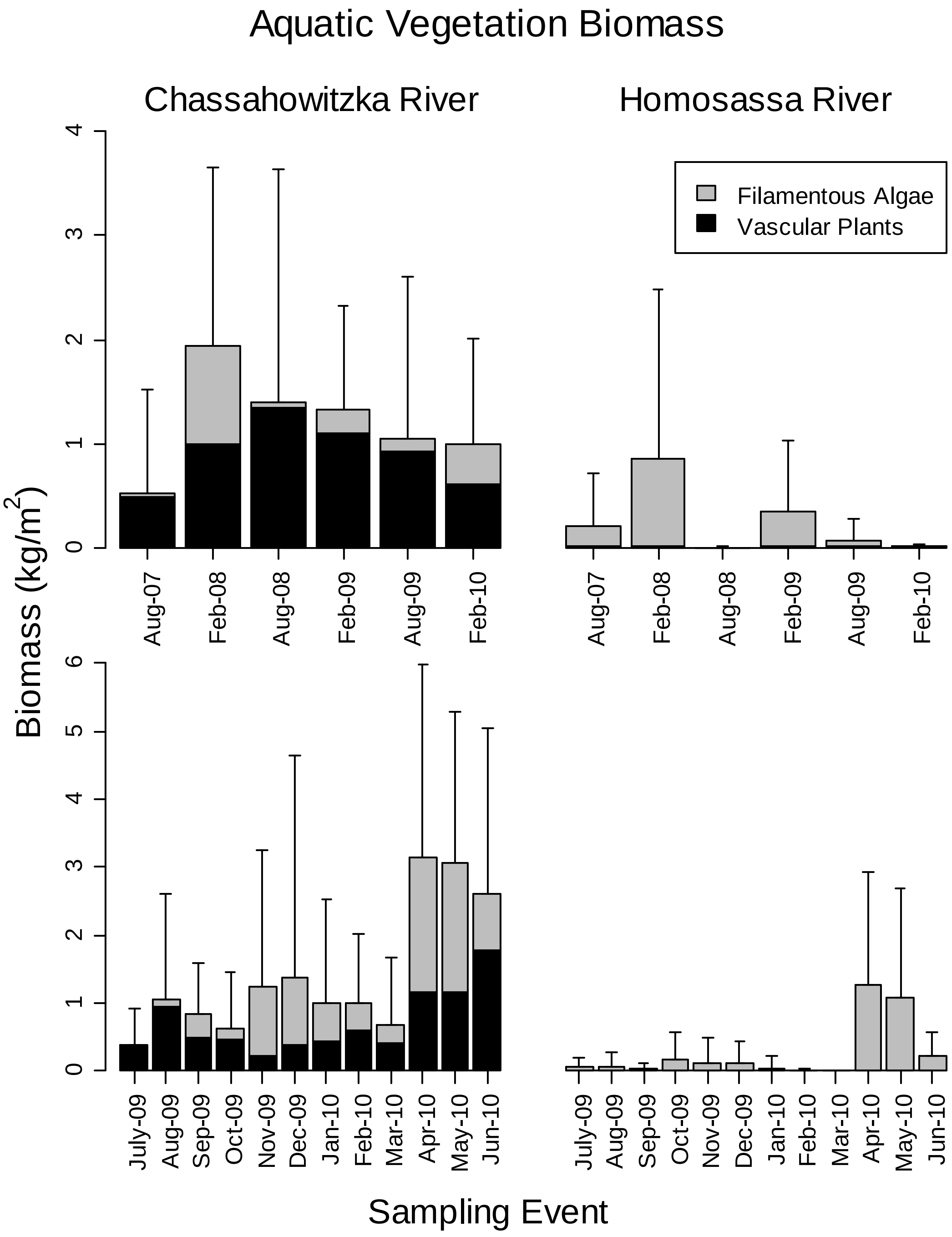

Figure 4-1. Mean estimated biomass of filamentous algae and macrophytes (measured as wet weight) within sampled reaches of the Chassahowitzka and Homosassa rivers during the period of study. Error bars represent one standard deviation of the mean total weight of aquatic vegetation.

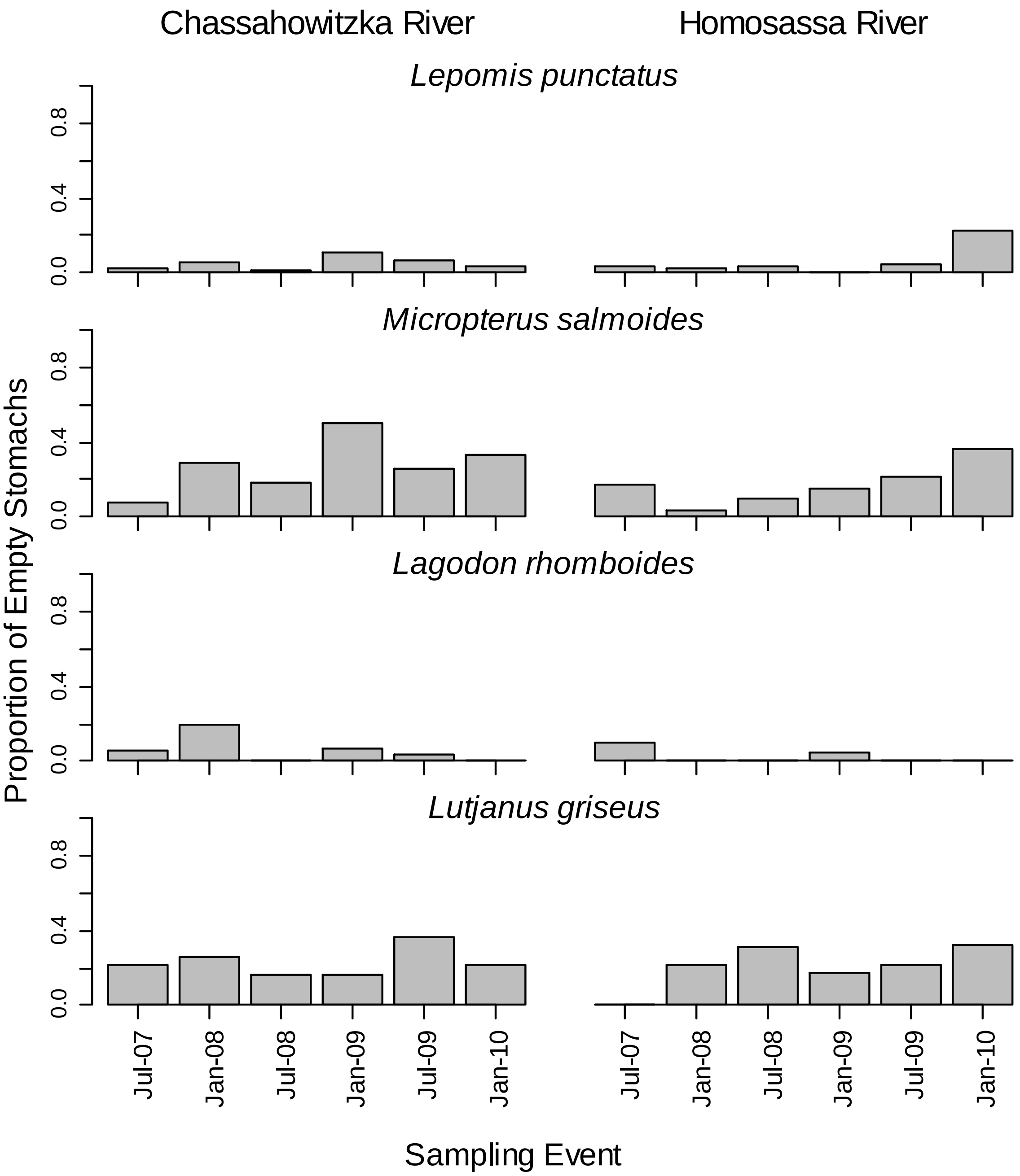

Figure 4-2. Seasonal and interannual patterns in mean proportion of empty stomachs of *Lepomis punctatus, Micropterus salmoides, Lagodon rhomboides*, and *Lutjanus griseus* from the Chassahowitzka and Homosassa rivers.

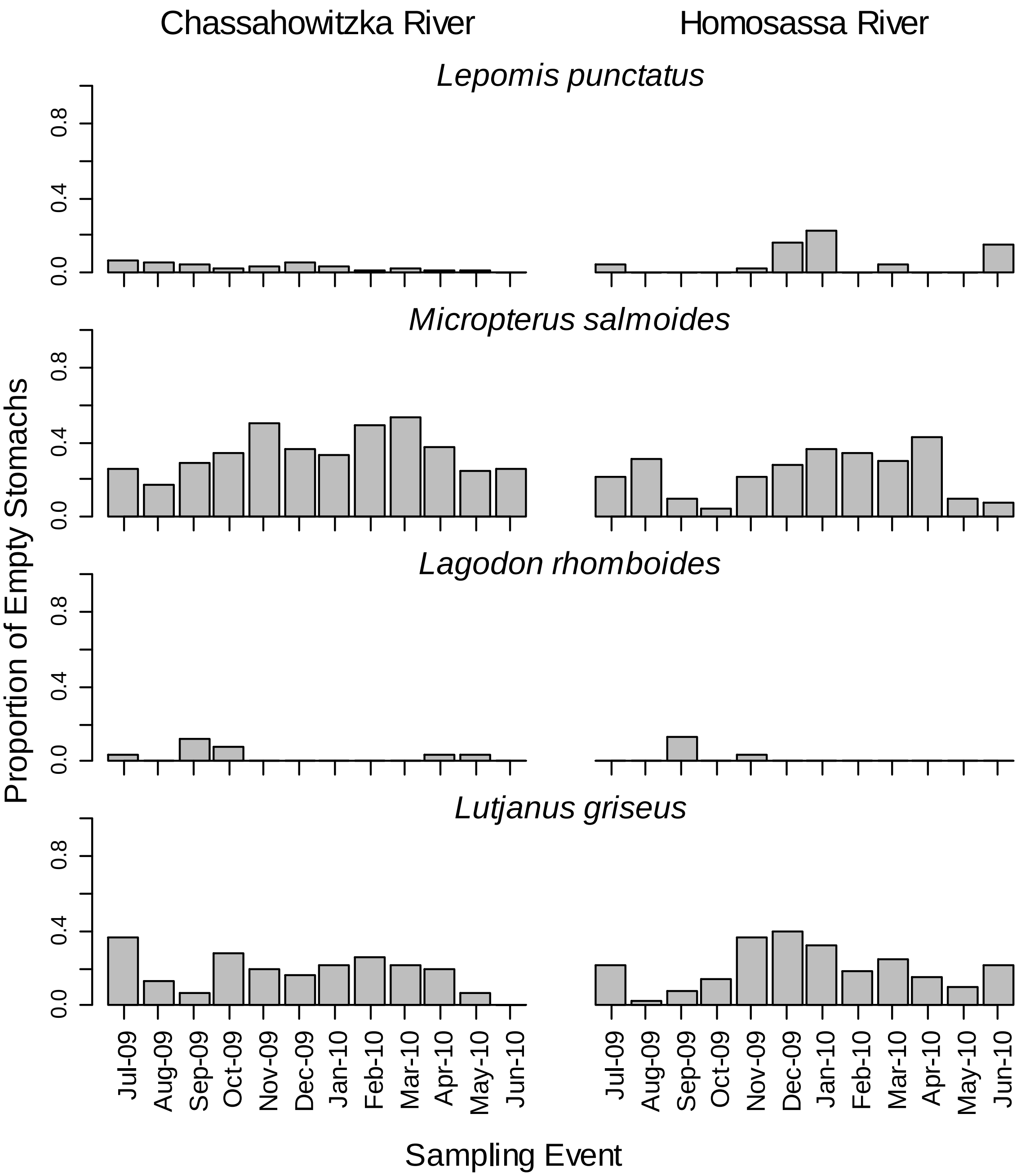

Figure 4-3. Intra-annual patterns in mean proportion of empty stomachs of *Lepomis punctatus, Micropterus salmoides, Lagodon rhomboides*, and *Lutjanus griseus* within the Chassahowitzka and Homosassa rivers.

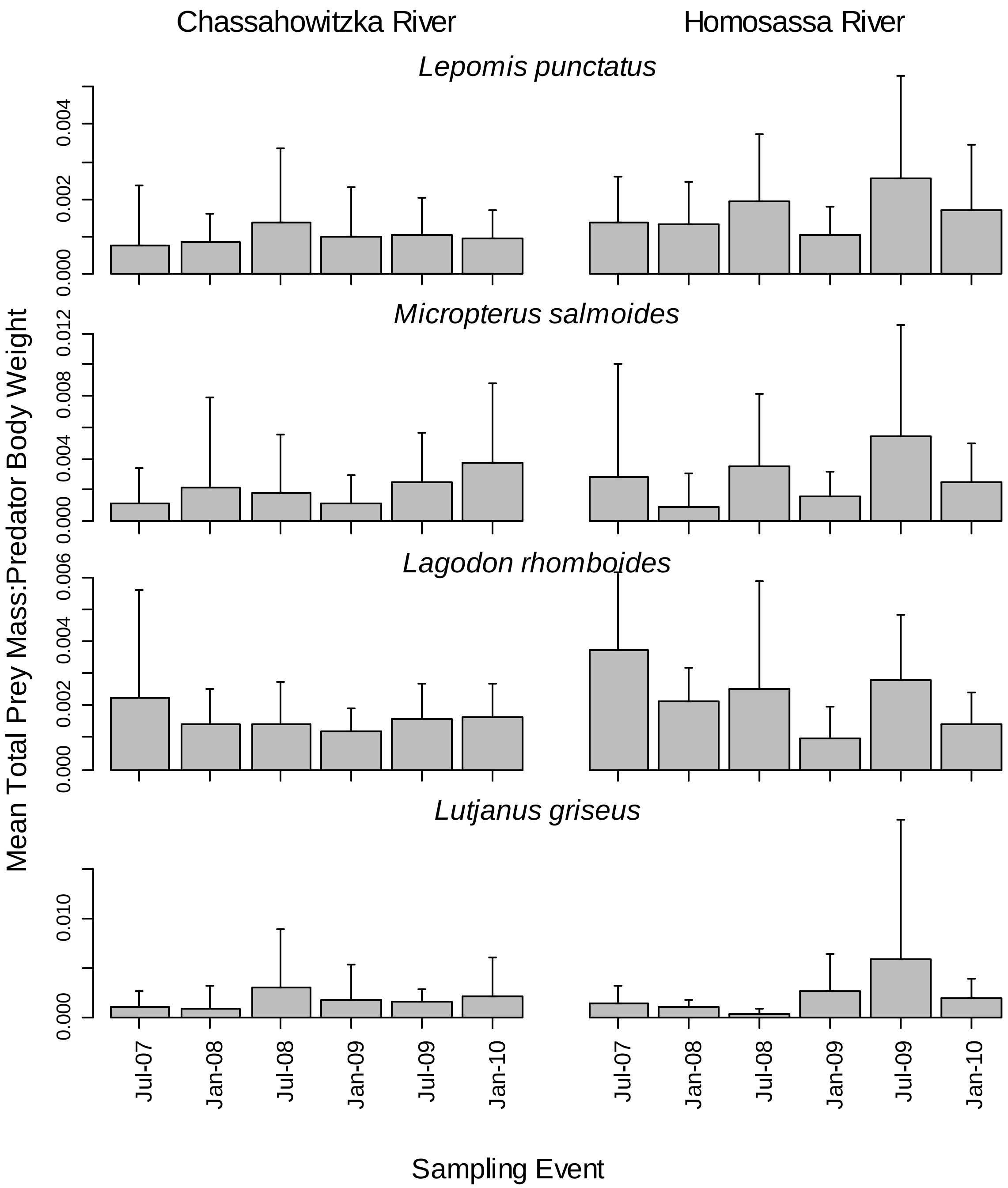

Figure 4-4. Seasonal and interannual patterns in mean total prey dry weight per predator body weight of *Lepomis punctatus, Micropterus salmoides, Lagodon rhomboides*, and *Lutjanus griseus* within the Chassahowitzka and Homosassa rivers.

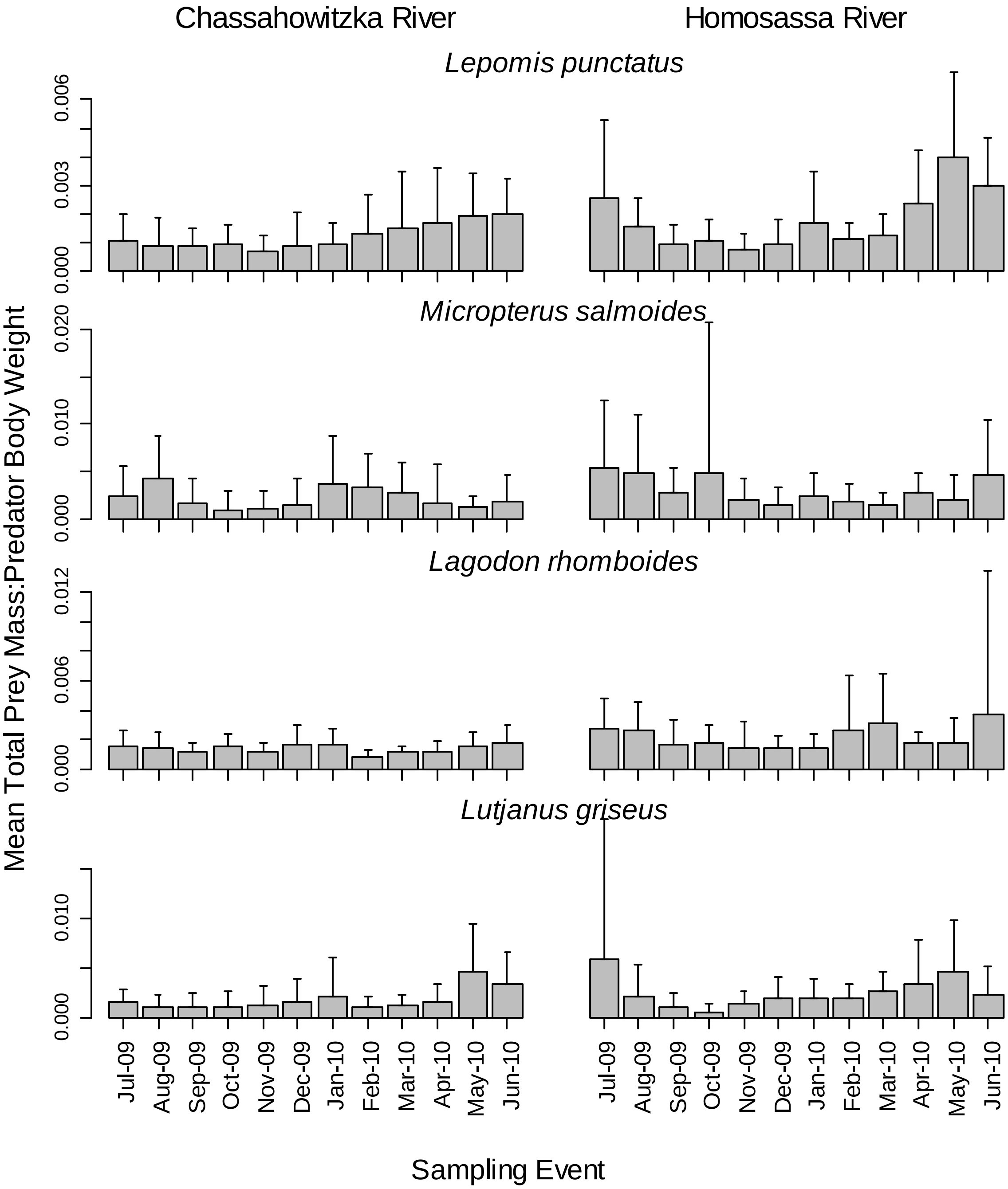

Figure 4-5. Intra-annual patterns in mean total prey dry weight per predator body weight of *Lepomis punctatus, Micropterus salmoides, Lagodon rhomboides*, and *Lutjanus griseus* within the Chassahowitzka and Homosassa rivers.

CHAPTER 5
VEGETATIVE HABITAT LOSS EFFECTS ON FISH AND INVERTEBRATE COMMUNITY STRUCTURE IN SPRING-FED, COASTAL RIVERS

Introduction

Autotrophs play a central role in the ecology of aquatic ecosystems by contributing to ecosystem production, modifying biogeochemical processes, and mediating biotic interactions (Carpenter and Lodge 1986, Jeppesen et al. 1998, Duarte 2002). Autotrophs, including rooted macrophytes, directly support the production of higher trophic levels and provide a fundamental control on the abundance and diversity of faunal organisms (Power 1995). Macrophytes provide a substrate for periphyton, which serve as a primary food base in many aquatic ecosystems (Jones et al. 1998). The production of periphyton is especially important in stream ecosystems (Minshall 1978), where downstream currents and low water residence times inhibit the production of phytoplankton and other suspended algae (Wetzel 2001). Furthermore, macrophytes link benthic substrates to the overlying water through the uptake of sediment-bound nutrients and transport of organic matter, minerals, and gases to both the water and benthic environments (Barko and James 1998, Caraco et al. 2006). Vegetative cover can decrease sediment erosion and resuspension by reducing water velocity and turbulence at the water-sediment interface (Gregg and Rose 1982, Barko and James 1998, Dodds and Biggs 2002), resulting in increased water clarity and light availability and providing a positive feedback loop for primary production. Macrophytes mediate predator-prey interactions between fishes and invertebrates by providing refuge habitat for prey populations and decreasing prey encounter rates of predators, allowing predator and prey populations to coexist at relatively high densities (Crowder and Cooper 1982). Through a combination of biological and physical controls on faunal organisms and the aquatic environment, primary producers have a strong influence on the structure of aquatic communities.

Human alterations of the landscape and associated changes in the physical and chemical properties of aquatic environments have resulted in a loss of macrophytes from many shallow aquatic ecosystems around the world (Duarte 2002). For example, in eutrophic systems, autotrophs capable of rapid nutrient uptake and growth can dominate and potentially exclude slow growing macrophytes with low nutrient uptake and assimilation rates (Duarte 1995). This phenomenon is exemplified by fast growing cyanobacteria and phytoplankton in nutrient-enriched lakes (Smith et al. 1999), macroalgae in nutrient-enriched estuaries (Valiela et al. 1997), and filamentous algae in nutrient-enriched streams (Huntsman 1948, Elwood et al. 1981). The effects of macrophyte loss and replacement by algal species on the faunal communities that they support are not currently well-understood. Population responses to vegetative habitat loss are likely to result from multiple coupled factors, including changes in food base (Chapter 4), loss of fish and invertebrate reproductive and juvenile rearing habitat, and altered trophic interactions.

Distinct shifts in the composition and biomass of primary producers have been documented within spring-fed, coastal rivers in Florida as a result of changes in watershed land-use, including increased agricultural and streamside development, and associated changes in streamflow and water quality (Frazer et al. 2006). Of particular concern is the rapid decline and extirpation of macrophytes, including *Vallisneria americana*, *Potamogeton* spp., and *Sagittaria kurziana*, from several systems, and the widespread proliferation of filamentous algae, including *Chaetomorpha* sp., *Gracilaria* sp., and *Lyngbya* sp. (Frazer et al. 2006, Stevenson et al. 2004). The loss of macrophytes which provide forage and refuge habitat may alter invertebrate grazer communities, predator/prey dynamics of fishes, and other important population-level interactions. Such alterations may lead to undesirable shifts in fish and invertebrate communities and possibly the loss of key species. Spring-fed rivers serve as model ecosystems to study the effects of vegetative habitat loss on fish and invertebrate populations due to their relatively steady streamflow, stable water temperatures, high rates of primary production (Odum 1953), and diverse communities of oligohaline and marine plants, algae, invertebrates and fishes (Herald and Strickland 1949, Odum 1957).

The purpose of this study was to develop an ecosystem model of a spring-fed, coastal river based on empirical data from the Chassahowitzka River, Florida for the purpose of predicting the responses of fish and invertebrate populations to changes in submersed aquatic vegetation (SAV) and resulting loss of habitat (extirpation of macrophytes and replacement with filamentous macroalgae). The model predictions were compared with the observed differences between the community structures of a highly vegetated river (the Chassahowitzka River) and one where rooted macrophytes have declined rapidly over the last decade and have been largely absent since 2006 (the Homosassa River). In addition, the predicted responses of fishes and invertebrate populations to an alternative policy option, macrophyte restoration, were compared with the predictions under a macrophyte extirpation scenario. These simulations will prove useful for understanding the ecological changes associated with vegetative habitat loss and the benefits of ecosystem restoration in terms of fish and invertebrate communities and the goods and services they provide.

Methods

To assess fish and invertebrate population responses to vegetative habitat availability in coastal rivers, I utilized a three-step assessment approach that included, (1) time-dynamic simulation of an ecosystem model based on empirical observations of a coastal river food web, (2) model validation by spatial comparative analysis of fish and invertebrate community structure in two coastal rivers with contrasting vegetative habitats, and (3) comparison of alternative policy options for coastal rivers including no action resulting in macrophyte extirpation versus ecosystem restoration resulting in increased macrophyte biomass in the Chassahowitzka River.

Trophic Mass-balance Model of a Coastal River Food Web

A trophic mass-balance model of the aquatic food web within the Chassahowitzka River was developed using the Ecopath with Ecosim software (Walters et al. 1997, Pauly et al. 2000, Christensen and Walters 2004). The software is available for free download at www.ecopath.org. The Ecopath modeling framework balances the annual production in biomass of individual trophic groups with losses to predation, harvest and migration, and net changes in biomass (Walters and Martell 2004). Model inputs for each trophic group included the proportion of the study area occupied, estimated biomass, production to biomass ratio, consumption to biomass ratio, prey composition, harvest information, and proportion of biomass contributed to the detrital pool versus biomass exported from the system. Table 5-1 lists the trophic groups of producers and consumers included in the model and the scientific names of the taxa comprising each trophic group. Empirical biomass estimates of trophic groups were acquired from vegetation quadrat sampling (macrophytes and filamentous algae), invertebrate sampling (benthic invertebrates, vegetation associated invertebrates, and amphipods), throw trap sampling (crayfish, blue crabs, mud crabs, and shrimp; Camp et al. 2011), block-netted seine sampling (freshwater and saltwater small-bodied fishes), boat electrofishing (lake chubsucker, *Lepomis* spp., largemouth bass, American eel, gar, striped mullet, pinfish, catfish, sheepshead, gray snapper, red drum and common snook), or data from long-term vegetation monitoring (periphyton; Frazer et al. 2006) and other sampling efforts (sediment diatoms; Frazer unpublished data). Methods for vegetation biomass estimation are described in Frazer et al. (2006), and methods for fish and invertebrate biomass estimation are described in the methods section of Chapter 3. All estimates were scaled to biomass in g per 100 m^2 (Table 3-1). The proportion of study area occupied was set equal to one for all trophic groups. Biomass estimates of each trophic group were based on seasonal estimates averaged across three years of sampling in the Chassahowitzka River, depending on whether the group was more abundant in winter (filamentous algae, select invertebrates and saltwater trophic groups) or summer (freshwater fishes and select invertebrate trophic groups) in the study reaches. Estimates of production to biomass ratios were determined from published literature (Table 5-2), or estimated from growth-at-age and mortality data (select freshwater fishes). Estimates of consumption to biomass ratios were determined from published literature (Table 5-2) or inferred from estimates of trophic groups within similar trophic guilds. A summary of the basic input parameters for the Ecopath model is provided in Table 5-3.

Empirical diet data for individual fish trophic groups were pooled across rivers and sampling events, and summarized by percent composition of total dry mass. Diet sampling methods are described in the methods section of Chapter 4. Diet information for invertebrates was synthesized from published literature; a list of references is included in Table 5-2. A predator-prey matrix was constructed to summarize the proportion of dietary items by prey group for each consumer trophic group (Table 5-4). To account for seasonality of migratory saltwater trophic groups foraging within the rivers, a gulf food base prey group was included in the model and diet composition of saltwater trophic groups was assumed to consist of 50% gulf food base. The contribution of saltwater fishes to the detritus in the rivers was assumed to be zero since these fishes utilize the rivers seasonally, and all freshwater trophic groups were assumed to contribute fully to the detrital pool (Table 5-5). Since the objective was to assess the effects of vegetative habitat on faunal populations, I did not include harvest in the model. The ecotrophic efficiency (proportion of production accounted for by predation, harvest, and net change in biomass within the model) of each trophic group was solved for using the Ecopath mass-balance parameterization. High ecotrophic efficiency values may imply competition among predators/fisheries for particular trophic groups, while low values imply low predation/fishing mortality on that trophic group, or inadequate accounting of sources of mortality in the model (Waters and Martell 2004).

Time-dynamic Simulation of Alternative Management Scenarios

The Ecosim module in the Ecopath with Ecosim program was used to simulate a long-term time series of trophic group biomass patterns under alternative policy options of no management action resulting in the continued decline and eventual extirpation of macrophytes from the Chassahowitzka River and replacement by seasonal production of filamentous algae, versus ecosystem restoration resulting in increased biomass of macrophytes and a reduction in filamentous algae biomass. The Ecosim framework simulates trophic group biomass rates of change over time based on gains from prey consumption times food conversion efficiency (proportion of prey consumed converted to biomass), and losses to mortality, including predation, fishing (assumed zero for the coastal river model), and unexplained natural mortality (Waters et al. 1997).

A 60-year time series was simulated for the Chassahowitzka River to simulate the continued decline and eventual extirpation of macrophytes and replacement by seasonally abundant filamentous algae. A forcing function was applied to macrophytes and associated periphyton trophic groups that simulated (1) an initial 20-year period of constant macrophyte biomass equal to the summer average over the study period in the Chassahowitzka River, (2) a 20-year period of steady linear decline in biomass from the initial biomass to complete extirpation, and (3) a 20-year period with macrophytes and associated periphyton extirpated from the system (Figure 5-1). A second forcing function was applied to filamentous algae that simulated (1) a 60-year period of cyclical filamentous algae blooms occurring seasonally based on observed monthly biomass patterns during year three of monitoring in the Chassahowitzka and Homosassa rivers (peak biomass was set equal to the mean observed winter biomass in the Chassahowitzka River) (Figure 5-1). The relative change in biomass of each trophic group was estimated as the difference between the average annual biomass of the initial 10-year period of the simulation and the average annual biomass of the terminal 10-year period of the simulation. The relative biomass change of each trophic group from the time-dynamic simulation was compared with the observed spatial differences in biomass between the Chassahowitzka and Homosassa rivers.

A long-term restoration scenario was simulated to examine the community-level effects of restoring macrophytes and reducing filamentous algae to observed pre-disturbance levels. Two forcing functions were used in this simulation. The first forcing function simulated (1) an initial 20-year period of constant macrophyte biomass equal to the summer average over the study period in the Chassahowitzka River, (2) a 20-year period of steady linear increase to twice the initial biomass, and (3) a 20-year terminal period with macrophyte biomass equal to twice the initial biomass (Figure 5-1). The first forcing function was also applied to periphyton associated with macrophytes. A second forcing function was applied to filamentous algae that simulated (1) an initial 20-year time series of filamentous algae equal to the observed seasonal pattern of filamentous algae biomass in the Chassahowitzka River with the peak production each year equal to the mean biomass observed during winter sampling, and (2) a 40-year period with constant filamentous algae biomass equal to the observed mean during summer in the Chassahowitzka River (approximately one-fifth the initial period peak winter biomass) (Figure 5-1). The mean annual biomass from the initial 10-year period of the simulation was compared with the terminal 10-year period mean annual biomass for each trophic group.

Results

The Ecopath trophic mass balance model illustrated the complexity of trophic interactions within the Chassahowitzka River (Figure 5-2). To balance the ecosystem model, several production to biomass estimates of invertebrates and small-bodied fishes were adjusted to higher values than the initial values from published literature

(Table 5-2). These results are not surprising due to the relatively warm water temperatures year-round, high nutrient loading, and the high primary production rates documented for spring-fed systems in Florida compared to other ecosystems (Odum 1957). The balanced trophic model predicted high transfer of invertebrate and small-bodied fish production to freshwater and marine fishes (Figure 5-3).

Time dynamic simulation of macrophyte extirpation and increased filamentous algae production predicted a strong negative response by many trophic groups of fishes and invertebrates, including gray snapper, saltwater catfishes, striped mullet, American eel, largemouth bass, *Lepomis* spp., lake chubsucker, freshwater small-bodied fishes, blue crabs, crayfish, mud crabs, grass shrimp, amphipods, and vegetation associated invertebrates (Figure 5-4). Positive responses to changes in submersed aquatic vegetation were predicted for several saltwater fishes (common snook, red drum, sheepshead, pinfish and small-bodied species), select freshwater fishes (Florida gar), and select invertebrates (sediment invertebrates).

Comparisons of observed spatial differences in mean trophic group biomass between the Chassahowitzka and Homosassa rivers (Figure 5-4) corroborated model predicted responses for many trophic groups, including common snook, red drum, sheepshead, saltwater small-bodied fishes, Florida gar, largemouth bass, *Lepomis* spp., lake chubsucker, blue crabs, crayfish, grass shrimp, amphipods, and benthic invertebrates. The predicted and observed changes in biomass were similar in direction and magnitude for a few trophic groups, including lake chubsucker, crayfish, and grass shrimp. The predicted magnitude of change was greater than the observed difference between rivers for largemouth bass, *Lepomis* spp., freshwater small-bodied fishes, and amphipods. The model predicted changes in biomass that were considerably less than observed spatial differences between rivers for multiple trophic groups, including common snook, red drum, sheepshead, saltwater small-bodied fishes, gar, and sediment associated invertebrates (Figure 5-4). In fact, the observed increase in biomass was often orders of magnitude greater than the predicted change. For several taxa/trophic groups (gray snapper, saltwater catfish, pinfish, striped mullet, American eel, mud crabs and vegetation associated invertebrates), the predicted response was opposite the observed differences in biomass between rivers (Figure 5-4).

Time-dynamic simulation of macrophyte restoration indicated a strong positive response by the majority of trophic groups to increased macrophyte and periphyton production (Figure 5-5), with the strongest responses predicted for catfish, pinfish, all freshwater fishes, crayfish, grass shrimp, and vegetation associated invertebrates. Restoration of aquatic vegetation was predicted to result in a decrease in biomass of mud crabs and amphipods as algae production decreased. Surprisingly, a couple of trophic groups were predicted to respond positively under either scenario of macrophyte extirpation or restoration, including common snook, red drum, sheepshead, pinfish, saltwater small-bodied fishes, Florida gar, and benthic invertebrates.

Discussion

The Ecopath trophic mass-balance model of the Chassahowitzka River indicated that invertebrates, particularly crustaceans, and small-bodied fishes are central to coastal river food webs, providing direct energy transfer from primary producers (periphyton, filamentous algae, and detritus from macrophytes, in particular) to large-bodied predators. The model estimated that the majority of invertebrate and small-bodied fish production was accounted for by fish predation within the river. These results are consistent with empirical diet patterns of fishes which demonstrated that freshwater and marine fishes are selectively foraging on crustaceans, vegetation associated invertebrates and small-bodied fishes (Chapter 4). Predation by fishes on these trophic groups is also validated by the observed declines in prey group biomass during winter sampling periods when marine predator density and biomass increased greatly (Chapter 3). Similar to these results, other researchers have reported high ecotrophic efficiencies of small-bodied fishes, crustaceans, and other invertebrate taxa in coastal aquatic food webs (Christensen 1995, Freire et al. 2008, Coll et al. 2009).

Key findings from time dynamic model simulation of macrophyte loss and extirpation included a predicted decline or extirpation of select freshwater and marine trophic groups (largemouth bass, *Lepomis* spp., lake chubsucker, freshwater small-bodied fishes, crayfish, and grass shrimp), increased biomass of select fish and invertebrate trophic groups (common snook, red drum, sheepshead, saltwater small-bodied fishes, and sediment invertebrates), and a resultant shift in faunal community composition. Overall, total invertebrate biomass was predicted to decrease by approximately 60% if macrophytes were extirpated from the Chassahowitzka River, primarily as a result of decreased biomass of crayfish and grass shrimp. Total fish biomass was predicted to decline by 11% as an indirect result of macrophyte extirpation. These results demonstrate that the loss of macrophytes from the coastal river ecosystem affects the composition of the aquatic community and food web structure, and results in a net decline in the biomass of fishes and invertebrates. Similar effects of macrophyte loss have been demonstrated for other freshwater (Bettoli et al. 1993) and marine communities (Deegan et al. 2002, Coll et al. 2011).

Macrophyte extirpation was predicted to result in a shift in the seasonality of primary production from a relatively steady perennial primary producer community with associated invertebrates and fishes to cyclical population dynamics related to boom-and-bust algae production and corresponding bottom-up responses of select invertebrate and fish populations. Empirical observations over the period of study (Chapter 3) indicated that vegetation biomass, freshwater invertebrate and fish trophic group biomass, and relative foraging success of fishes (Chapter 4) was less variable seasonally and between years in the Chassahowitzka River, while invertebrate and freshwater fish biomass in the Homosassa River demonstrated seasonal patterns related to the availability of filamentous algae habitat. Monthly monitoring of vegetation and fishes in the Homosassa River during year three of the study showed that large-scale algal production during March and April resulted in a sharp increase in young-of-the-year freshwater and saltwater fishes (Chapter 3); however, the longer-term response of invertebrate and fish communities was not measured since the widespread algae blooms occurred during the end of the period of study. Based on ecosystem model predictions and empirical observations, faunal population dynamics are expected to be more stable in a river dominated by aquatic macrophytes versus one dependent on the production of filamentous algae, exclusively.

Observed differences in the estimated biomass of select species between the Chassahowitzka and Homosassa rivers validated several model predictions under the macrophyte extirpation scenario, including losses of lake chubsucker, crayfish and grass shrimp from the Homosassa River; decreased biomass of largemouth bass, *Lepomis* spp., freshwater small-bodied fishes, blue crabs, and amphipods in the

Homosassa River compared to the Chassahowitzka River; increased biomass of common snook, red drum, sheepshead, saltwater small-bodied fishes, Florida gar, and benthic invertebrates in the Homosassa River; and observed boom-and-bust dynamics of invertebrates associated with filamentous algae and fishes that forage on these invertebrate groups.   Overall, the Ecosim model accurately predicted the direction of faunal group responses for most freshwater and marine taxa; however, the magnitude of change was inaccurate for nearly all taxa measured with the exception of those taxa that were found to be nearly extirpated from the Homosassa River (lake chubsucker, crayfish, and grass shrimp).

The anomalous predictions in species biomass patterns provide interesting cases of counterintuitive population responses. The increase in biomass of select saltwater fishes is not surprising since their recruitment may be independent of the habitat and trophic dynamics within the rivers and the Homosassa River is deeper, has greater discharge, and provides a larger volume of freshwater that serves as winter habitat for thermally sensitive species (Odum 1953). The contradictory responses of freshwater trophic groups, on the other hand, present areas of potential future ecological research. For example, the observed biomass of Florida gar in the Homosassa River was 72 times greater than in the Chassahowitzka River; however, the ecosystem model predicted a change in biomass that was considerably less than the observed difference. One possible explanation is increased spawning success of Florida gar. I observed gar successfully spawning on filamentous algae patches during the spring of year three and captured a higher abundance of young-of-the-year in the following sampling events. The response of gar to changes in vegetative habitat may be indicative of a "skeleton in the closet” effect (Walters and Martell 2004), where the trophic group’s recruitment is suppressed in one ecosystem state (in this case a highly structured macrophyte dominated system) and whose population bottleneck is released in an altered state (an unstructured algae dominated system). Alternative hypotheses that may account for the observed difference in biomass include improved foraging success in an unstructured river or high tolerance to decreased water quality (Kushlan 1974).

The ecosystem model incorrectly predicted the local extinction of several freshwater fish trophic groups in response to the loss of macrophytes. Largemouth bass, *Lepomis* spp. and freshwater small-bodied fishes demonstrated a lowered biomass in the Homosassa River compared to the Chassahowitzka River; however, the trophic group declines were less than predicted by the model. Since macrophytes have been largely absent from the Homosassa River for approximately the last five years, it is possible that the full extent of population responses to vegetative habitat loss were not detected over the last three years of study. The response may be much greater following several generations of decreased recruitment and other changes in population dynamics (Lauretta, unpublished data). While I observed relatively large numbers of young-of-the-year largemouth bass and *Lepomis* spp. during each year in both rivers, there was a clear difference in the number of juveniles surviving to larger age classes. In the Chassahowitzka River, a greater proportion of juveniles survived compared to the Homosassa River, where older individuals were rare. Alternatively, prey switching by largemouth bass and *Lepomis* spp. could explain the sustained populations in the Homosassa River, as evidenced by spatial differences in diet composition between populations in the rivers, and the seasonal differences in prey composition in the

Homosassa River related to availability of filamentous algae and associated invertebrate prey groups (Chapter 4).

The loss of grazers and detritivores from coastal rivers, including lake chubsucker and crayfish, could result in a negative feedback on macrophyte production. For example, lake chubsucker require vegetative habitat to successfully reproduce and forage, and were historically common in the Homosassa River when macrophytes communities were prevalent (Herald and Strickland 1949). The decline of this habitat likely had negative effects on chubsucker reproduction, foraging success, and survival, potentially leading to the extirpation of this species from portions of the river. The population decline of this key fish herbivore could have decreased grazing of periphyton on plant stems, resulting in increased shading of plants, which may have further accelerated plant loss in the ecosystem (Roberts et al. 2003), resulting in a vegetative community comprised exclusively of seasonally abundant filamentous algae.

Alternative hypotheses for ecosystem change that were not captured in the trophic dynamic model include shifts in system energy dynamics, such as increased allochthonous input and terrestrially based prey items. Diet information for several species of freshwater fishes (e.g., largemouth bass and *Lepomis* spp.) indicated that individuals within the Homosassa River consumed terrestrial organisms, including lizards, waterfowl and terrestrial insects, during summer months when producer and invertebrate biomass was relatively low (Chapter 4). In addition, observed differences in mud crabs and vegetation associated invertebrates, particularly gastropods, between systems and the opposite population trends from the predicted responses demonstrated that the population ecology (feeding and production) of these trophic groups was not likely accurately represented in the ecosystem model. Additional studies that would increase the understanding of trophic dynamics in the coastal rivers and likely improve the predictability of the ecosystem model include diet composition of small-bodied fishes and invertebrates and annual production estimates of producer and invertebrate trophic groups.

Macrophyte restoration was predicted to have beneficial effects on the majority of fish and invertebrate populations, especially freshwater trophic groups, with negative effects predicted for relatively few groups, including mud crabs and amphipods, in response to decreased algae production. These results demonstrated the importance of macrophytes in sustaining the freshwater aquatic food web, as well as the benefit of macrophyte habitat to saltwater fish taxa and the aquatic communities as a whole. Since several of these trophic groups support recreational fisheries within the rivers and the Gulf of Mexico, the restoration of macrophytes may have beneficial economic effects as well as ecological benefits. These rivers represent important juvenile rearing and overwintering habitats for economically valuable marine stocks, including common snook, red drum, and gray snapper. Habitat improvement in the river may benefit these stocks through increased juvenile recruitment resulting from greater food availability and lowered predation risk in macrophyte dominated habitats, as well as increased adult survival during winter periods when water temperatures in the Gulf of Mexico can drop below species tolerance thresholds. Overall, macrophyte restoration was predicted to result in an increase in total invertebrate biomass of approximately 152% and an increase in total fish biomass of approximately 73%. In addition to benefits to fish and invertebrate populations, the restoration of macrophytes may help improve and maintain water quality within the rivers, providing a positive feedback for ecosystem primary production, and increasing the water quality and aesthetic value of the rivers to the streamside communities and recreational boaters.

Table 5-1. Trophic groups and taxa composition included in the Ecopath trophic mass-balance model of the Chassahowitzka River food web.

Trophic Group	**Taxa Identification**
Common snook	*Centropomis undecimalis*
Red drum	*Sciaenops ocellatus*
Gray snapper	*Lutjanus griseus*
Sheepshead	*Archosargus probatocephalus*
Catfish	*Ariopsis felis, Bagre marinus*
Pinfish	*Lagodon rhomboides*
Striped mullet	*Mugil cephalus*
Saltwater small-bodied fishes	*Anchoa* sp., *Gobiosoma* sp., *Leiostomus* sp., *Microgobius* sp., *Strongylura* spp., *Syngnathus* sp., *Trinectes* sp.
Gar	*Lepisosteus platyrhincus, Lepisosteus osseus*
American eel	*Anguilla rostrata*
Largemouth bass adults	*Micropterus salmoides* ages 1-6
Largemouth bass juveniles	*Micropterus salmoides* age 0
Lepomis spp. adults	*L. punctatus, L. macrochirus, L. microlophus, L. gulosus* ages 1-3
Lepomis spp. juveniles	*L. punctatus, L. macrochirus, L. microlophus, L. gulosus* age 0
Lake chubsucker adults	*Erimyzon sucetta* ages 1-3
Lake chubsucker juveniles	*Erimyzon sucetta* age 0
Freshwater small-bodied fishes	*Lucania* spp., *Menidia* sp., *Notropis* spp., *Fundulus* spp.
Blue crab	*Callinectes sapidus*
Crayfish	Cambaridae
Mud crabs	Grapsidae, Xanthidae
Grass shrimp	*Palaemonetes* spp.
Amphipods	*Corophium sp., Gammarus spp., Grandidierella sp., Hyalella sp.*
Vegetative invertebrates	Diptera larvae/pupae, Gastropoda, Isopoda, Tanaidacae
Benthic invertebrates	Bivalva, Nematoda, Oligochaeta, Ostracoda, Polychaeta
Periphyton	unknown taxa composition
Filamentous alage	*Chaetomorpha* sp., *Gracilaria* sp., *Lyngbya* sp.
Vascular plants	*Vallisneria americana, Potamogeton* spp., *Hydrilla verticillata, Myriophyllum spicatum, Najas guadalupensis, Zanichelli* sp.
Sediment diatoms	unknown taxa composition
Detritus	unknown composition

Table 5-2. Data sources for the Ecopath trophic mass balance of the Chassahowitzka River food web.

Trophic Group	Biomass	P/B	Q/B	Diet
Common snook	Empirical capture-recapture	Walters et al. 2008	Walters et al. 2008	Empirical gut analysis
Red drum	Empirical capture-recapture	Walters et al. 2008	Walters et al. 2008	Empirical gut analysis
Gray snapper	Empirical capture-recapture	Walters et al. 2008	Walters et al. 2008	Empirical gut analysis
Catfish	Empirical capture-recapture	Walters et al. 2008	Walters et al. 2008	Empirical gut analysis
Sheepshead	Empirical capture-recapture	Walters et al. 2008	Walters et al. 2008	Empirical gut analysis
Pinfish	Empirical capture-recapture	Walters et al. 2008	Walters et al. 2008	Empirical gut analysis
Striped mullet	Empirical capture-recapture	Walters et al. 2008	Walters et al. 2008	Empirical gut analysis
Florida gar	Empirical capture-recapture	Equal to 1/2 adult bass	Equal to adult bass	Empirical gut analysis
American eel	Empirical capture-recapture	Equal to 1/2 adult bass	Equal to adult bass	Empirical gut analysis
Largemouth bass adults	Empirical capture-recapture	Estimated from growth	Estimated from growth	Empirical gut analysis
Largemouth bass juveniles	Empirical capture-recapture	Estimated from growth	Estimated from growth	Empirical gut analysis
Lepomis adults	Empirical capture-recapture	Estimated from growth	Estimated from growth	Empirical gut analysis
Lepomis juveniles	Empirical capture-recapture	Estimated from growth	Estimated from growth	Empirical gut analysis
Lake chubsucker adults	Empirical capture-recapture	Estimated from growth	Estimated from growth	Empirical gut analysis
Lake chubsucker juveniles	Empirical capture-recapture	Estimated from growth	Estimated from growth	Empirical gut analysis
SW small-bodied fishes	Empirical seine removal	Walters et al. 2008	Walters et al. 2008	Empirical gut analysis
FW small-bodied fishes	Empirical seine removal	Assumed equal to SWSB fishes	Assumed equal to SWSB Fishes	Empirical gut analysis
Blue crabs	Camp et al. 2010	Walters et al. 2008 (adjusted)	Walters et al. 2008 (adjusted)	Dittel et al. 2006, Reichmuth et al. 2009, Seitz et al. 2005, Mascaro et al., Rosas et al. 1994
Crayfish	Camp et al. 2010	Equal to blue crabs	Equal to blue crabs	Gutierrez-Yurrita et al. 1998
Mud crabs	Camp et al. 2010	Equal to blue crabs (adjusted)	Equal to blue crabs (adjusted)	Kneib and Weeks 1990
Shrimp	Camp et al. 2010	Walters et al. 2008	Walters et al. 2008	Collins 1999, Morgan 1980, Costantin and Rossi 2001
Amphipods	Empirical invert samples	Kevrekidis et al. 2009, Subida et al. 2005	Equal to shrimp	MacNeil et al. 1997, Duffy and Harvilicz 2001
Vegetative invertebrates	Empirical invert samples	Robertson 1979 (adjusted)	2x P/B	Assumed 100% grazers
Benthic invertebrates	Empirical invert samples	Robertson 1979 (adjusted)	2x P/B	Assumed 50% detritivores/ 50% grazers
Periphyton	Frazer et al. 2006	Assumed equal to 10	NA	NA
Filamentous Algae	Empirical quadrat samples	Assumed equal to 20	NA	NA
Plants	Empirical quadrat samples	Walters et al. 2008	NA	NA
Sediment diatoms	Frazer unpublished data	Unpublished data	NA	NA

Table 5-3. Basic inputs for the Ecopath trophic mass-balance model of the Chassahowitzka River food web.

Group name	Habitat area (fraction)	Biomass (g/100m^2)	P/B (annual)	Q/B (annual)
Common snook	1	15	1.5	4.0
Red drum	1	1	1.0	3.0
Gray snapper	1	1,050	2.5	40.0
Catfish	1	10	0.8	7.6
Sheepshead	1	1	1.0	3.0
Pinfish	1	160	1.0	8.0
Striped mullet	1	131	0.8	8.0
Florida gar	1	1	0.5	5.0
American eel	1	42	0.5	5.0
Largemouth bass adults	1	510	1.0	5.0
Largemouth bass juveniles	1	89	5.0	20.5
Lepomis adults	1	205	1.0	5.0
Lepomis juveniles	1	122	6.0	16.9
Lake chubsucker adults	1	45	1.0	20.0
Lake chubsucker juveniles	1	38	6.0	59.7
SW small-bodied fishes	1	890	2.7	15.0
FW small-bodied fishes	1	800	2.7	15.0
Blue crabs	1	1,520	3.0	8.5
Crayfish	1	2,270	2.5	8.5
Mud crabs	1	2,050	4.0	12.0
Shrimp	1	535	2.4	20.0
Amphipods	1	2,350	9.0	20.0
Vegetative invertebrates	1	850	20.0	40.0
Benthic invertebrates	1	250	42.0	85.0
Gulf foodbase	1	40,000	1.0	NA
Periphyton	1	29,150	10.0	NA
Filamentous algae	1	53,150	20.0	NA
Plants	1	116,500	7.0	NA
Sediment diatoms	1	1,750	150.0	NA
Detritus	1	30,000	NA	NA

Table 5-4. Diet composition of consumers within the Chassahowitzka and Homosassa rivers, Florida.

	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	Common snook																								
2	Red drum																								
3	Gray snapper	0.065									0.080														
4	Catfish																								
5	Sheepshead																								
6	Pinfish	0.020									0.050														
7	Striped mullet	0.005							0.100																
8	Florida gar																								
9	American eel																								
10	Largemouth bass adults																								
11	Largemouth bass juveniles										0.020														
12	Lepomis adults	0.035	0.005								0.026														
13	Lepomis juveniles	0.035	0.005								0.026	0.019													
14	Lake chubsucker adults										0.006														
15	Lake chubsucker juveniles										0.006														
16	SW small-bodied fishes	0.271	0.278	0.039	0.100				0.150		0.148	0.204													
17	FW small-bodied fishes	0.030	0.010	0.020					0.400	0.010	0.100	0.487		0.035											
18	Blue crabs	0.025	0.075	0.057		0.014	0.001		0.250	0.115	0.080		0.036				0.069	0.019							
19	Crayfish		0.005	0.035			0.021		0.070	0.433	0.418	0.039	0.056	0.017			0.028								
20	Mud crabs	0.010	0.075	0.173		0.034	0.012			0.336	0.020	0.048	0.127	0.052				0.028							
21	Shrimp	0.005	0.014	0.011	0.400		0.001		0.020		0.020	0.097	0.018	0.017			0.004								
22	Amphipods		0.024	0.162		0.060	0.085			0.049		0.095	0.235	0.282	0.351	0.207	0.256	0.641							
23	Vegetative invertebrates		0.005	0.004		0.019	0.025		0.010	0.029		0.010	0.472	0.495			0.037	0.293	0.167	0.400		0.100			
24	Benthic invertebrates		0.005			0.374	0.014	0.010		0.029			0.056	0.102	0.098	0.119	0.107	0.019	0.167	0.100	0.100	0.100			
25	Gulf foodbase	0.500	0.500	0.500	0.500	0.500	0.500	0.500									0.500		0.500						
26	Periphyton														0.539	0.661						0.300	0.050	0.500	
27	Filamentous algae							0.190							0.012	0.013					0.800	0.300	0.950	0.400	
28	Plants						0.340																	0.100	
29	Sediment diatoms																								0.500
30	Detritus							0.300											0.167	0.500	0.100	0.200			0.500

Prey groups are listed in rows, and predator groups are listed in columns with reference numbers corresponding to the group name listed in column 1.

Table 5-5. Detrital fate matrix for the Ecopath trophic mass-balance model of the Chassahowitzka River food web.

Source \ Fate	Detritus	Export	Sum
Common snook	0	1	1
Red drum	0	1	1
Gray snapper	0	1	1
Catfish	0	1	1
Sheepshead	0	1	1
Pinfish	0	1	1
Striped mullet	0	1	1
Florida gar	1	0	1
American eel	1	0	1
Largemouth bass adults	1	0	1
Largemouth bass juveniles	1	0	1
Lepomis adults	1	0	1
Lepomis juveniles	1	0	1
Lake chubsucker adults	1	0	1
Lake chubsucker juveniles	1	0	1
SW small-bodied fishes	0	1	1
FW small-bodied fishes	1	0	1
Blue crabs	1	0	1
Crayfish	1	0	1
Mud crabs	1	0	1
Shrimp	1	0	1
Amphipods	1	0	1
Vegetative invertebrates	1	0	1
Benthic invertebrates	1	0	1
Gulf foodbase	0	1	1
Periphyton	1	0	1
Filamentous algae	1	0	1
Plants	1	0	1
Detritus	0	1	1

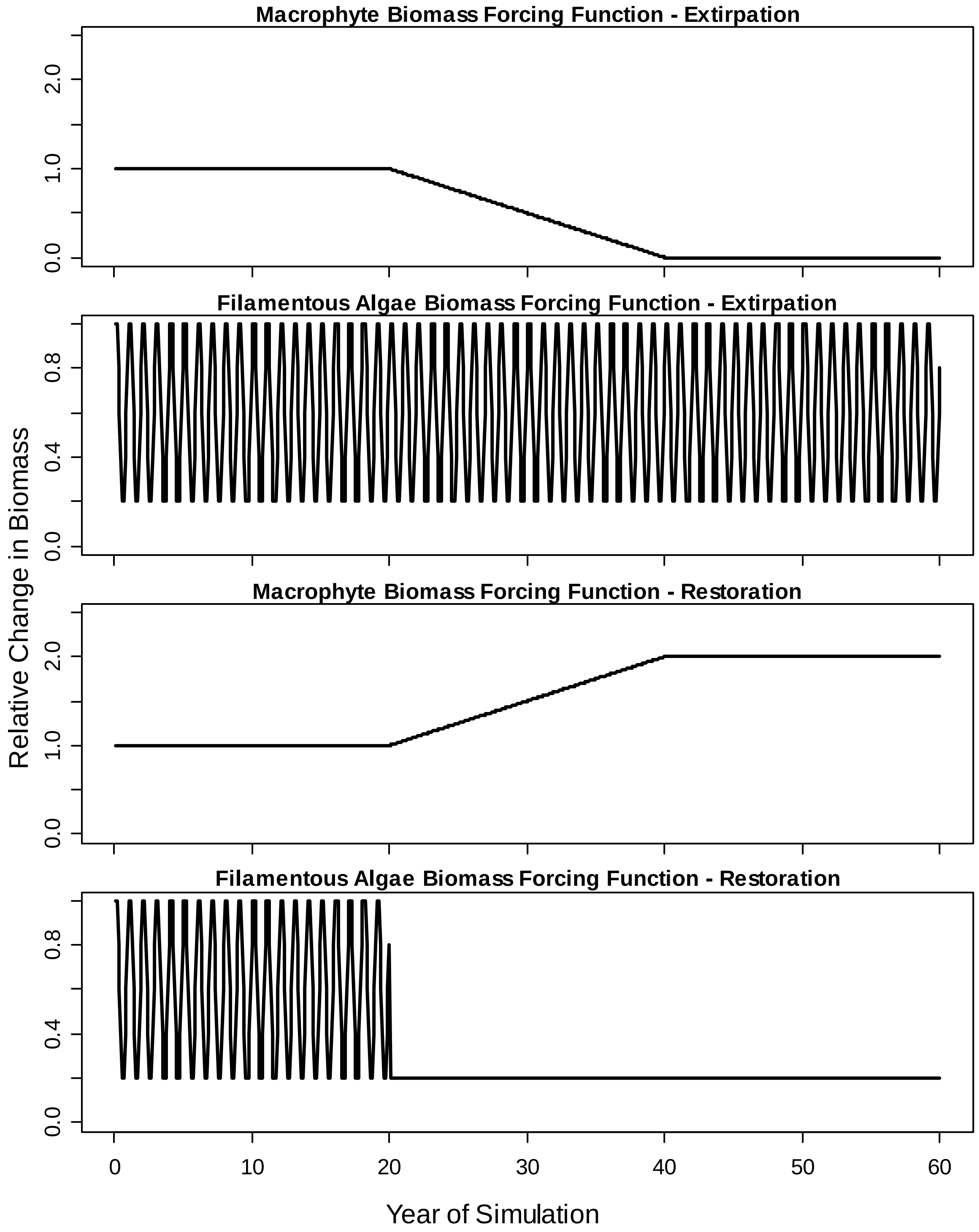

Figure 5-1. Ecosim forcing functions used to simulate changes in primary production within the Chassahowitzka River, Florida under alternative management scenarios of macrophyte extirpation versus restoration.

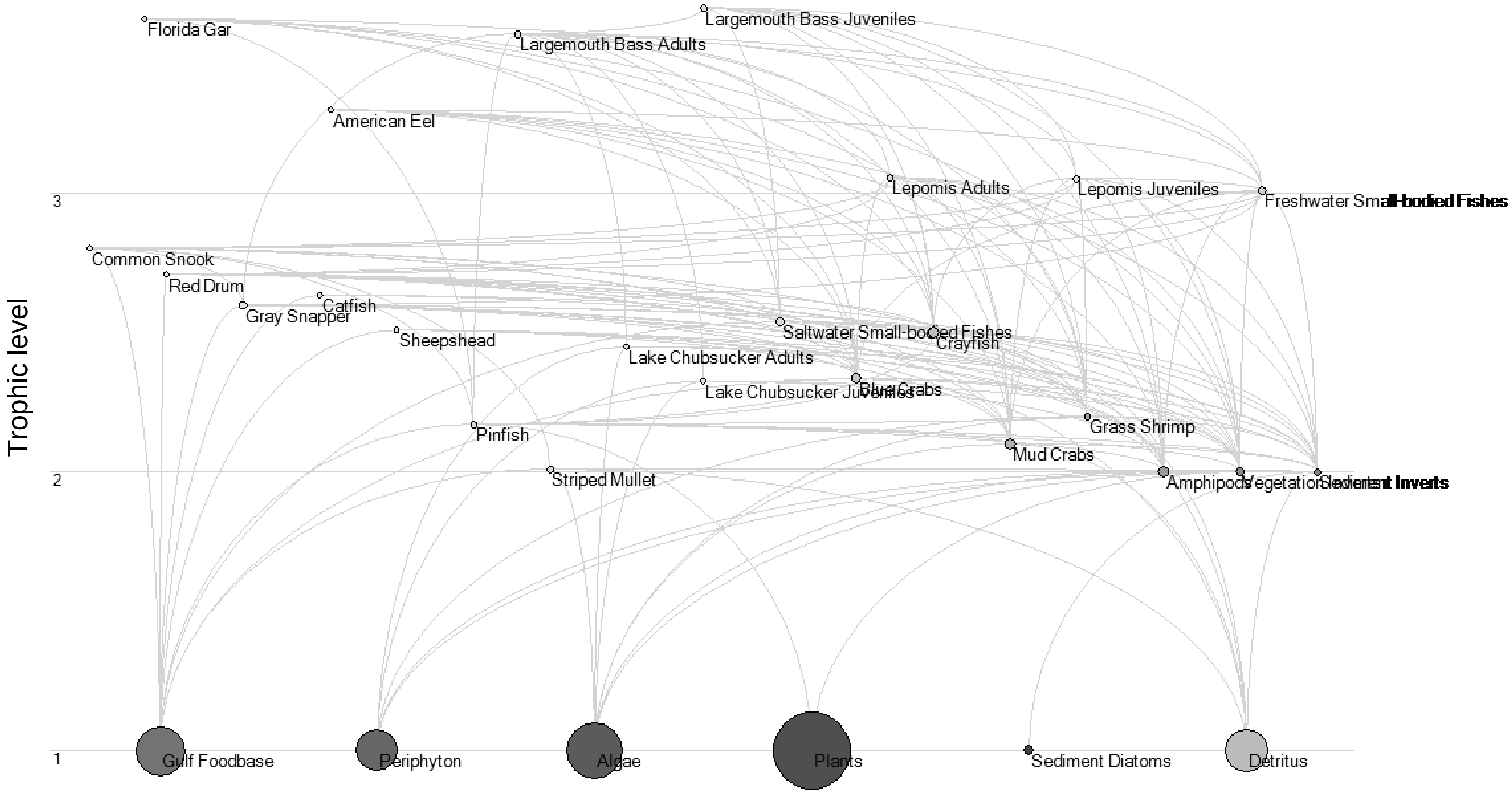

Figure 5-2. Ecopath trophic flow diagram of the Chassahowitzka River. The size of the circle is relative to the biomass of the trophic group.

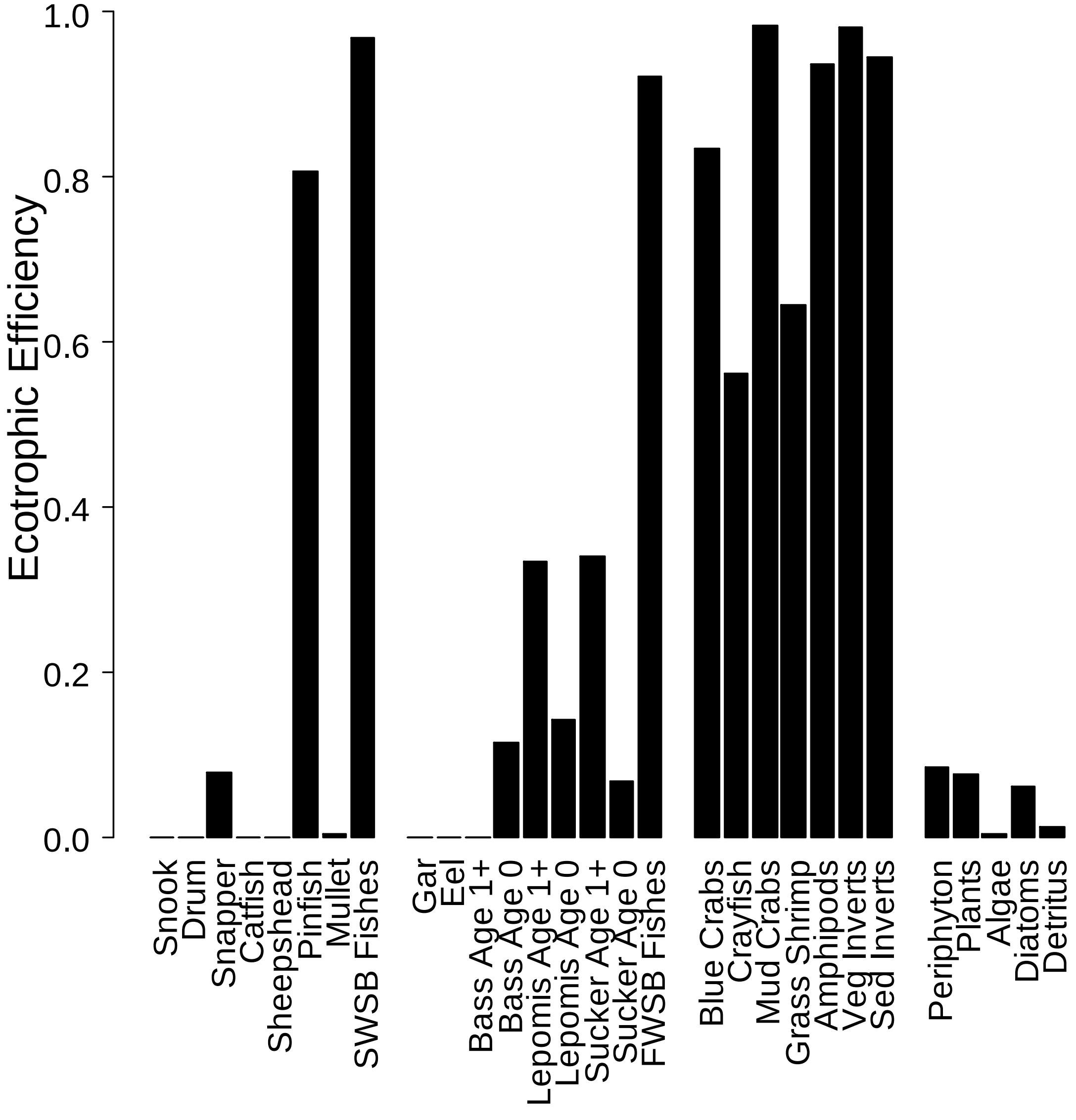

Figure 5-3. Predicted ecotrophic efficiency (proportion of production consumed by predators) of trophic groups within the Chassahowitzka River food web model.

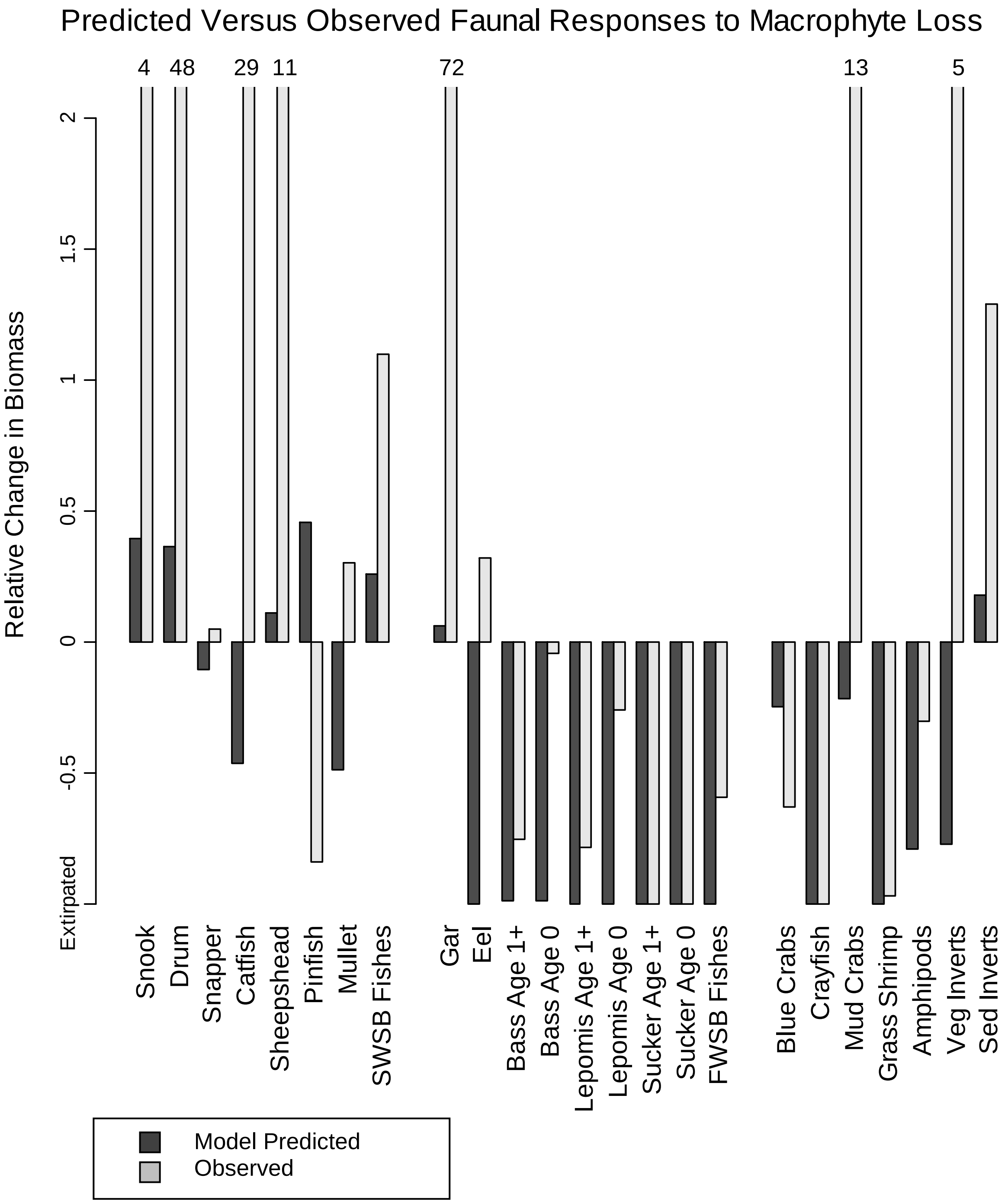

Figure 5-4. Comparison of time dynamic ecosystem model predicted changes in mean annual biomass of trophic groups versus observed spatial differences between the Chassahowitzka and Homosassa rivers.

Predicted Community Responses to Alternative Policies

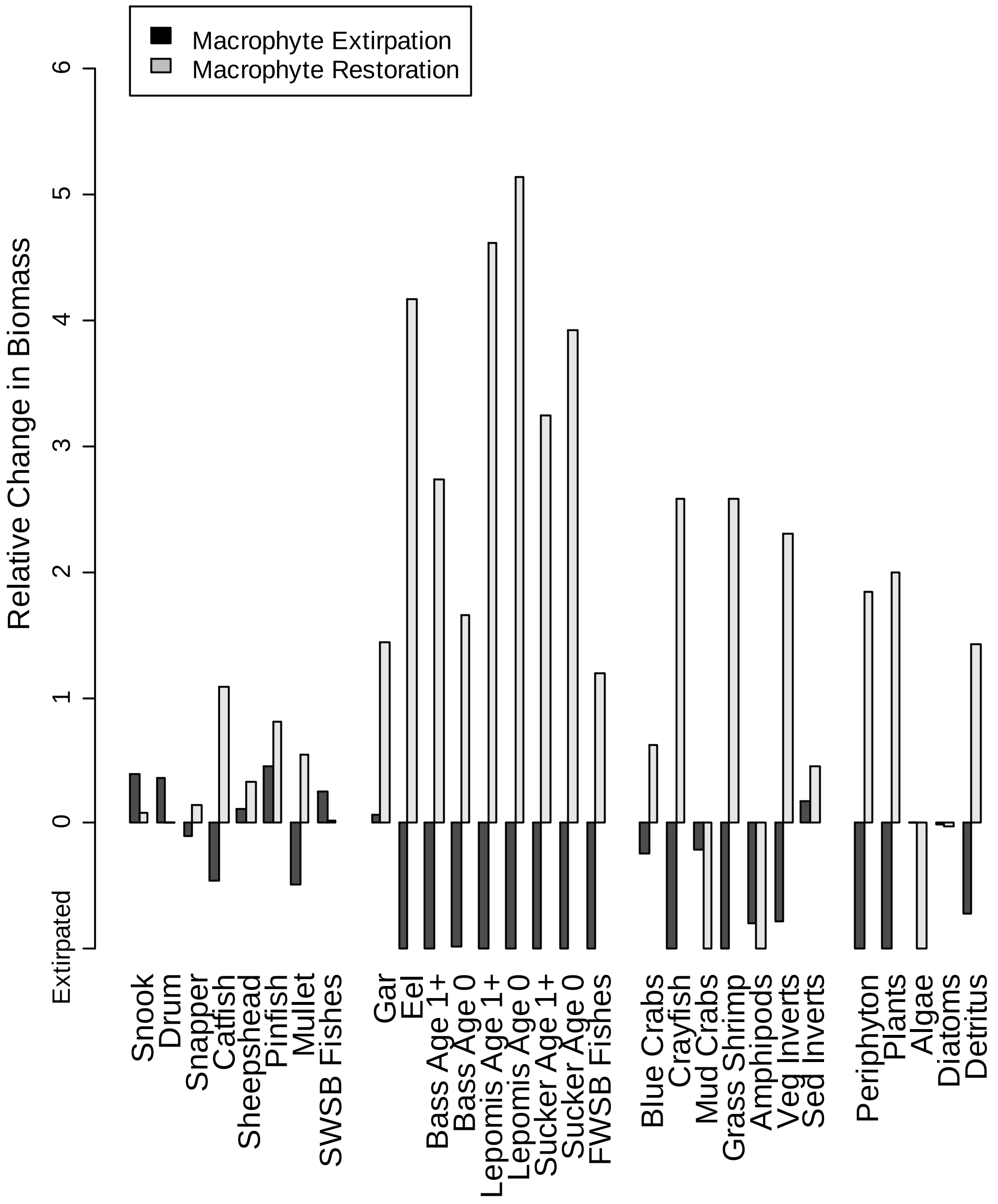

Figure 5-5. Comparison of time dynamic ecosystem model predicted community responses to the extirpation and restoration of macrophytes in the Chassahowitzka River.

CHAPTER 6
SYNTHESIS AND FUTURE RESEARCH

Spring-fed systems in Florida have been historically described as homeostatic in their chemical, physical and biological characteristics (Odum 1957). The data collected during this study demonstrated that spring-fed, coastal rivers are spatially and temporally dynamic in vegetative, invertebrate, and fish community composition and biomass. Based on river-wide comparisons of faunal community composition, biomass, diet of fishes, and ecosystem time-dynamic simulation, I infer that vegetative habitat loss negatively affects species that rely on this habitat type for foraging, refuge or reproduction, including crayfish, grass shrimp, small-bodied freshwater fishes, lake chubsucker, pinfish, spotted sunfish and largemouth bass. Species that do not have a strong affinity for structural habitat (SAV in particular) will be less affected by large-scale changes in vegetation, such as mud crabs, select saltwater small-bodied fishes, gray snapper, Florida gar and longnose gar (*Lepisosteus osseus*). The observed differences and model predicted responses in population biomass and diet of fishes are evidence that changes in vegetative habitat affect individual species disproportionately, and continued changes are likely to alter the fish and invertebrate communities in these coastal ecosystems.

Other researchers have documented community-level shifts associated with the removal of key habitat components in aquatic ecosystems. Sass et al. (2006) demonstrated that the removal of a structurally complex habitat (course woody debris) in a Wisconsin lake significantly impacted species interactions and decreased fish abundance, survivorship, recruitment and growth, resulting in a shift in the community composition of fishes. The results of this research demonstrated similar effects of structural habitat loss on fish populations, although the production loss from the removal of plants may have disproportionately affected grazer communities in coastal rivers, compared to the removal of woody debris observed by Sass et al. (2006). Bettoli et al. (1993) showed that removal of the macrophyte community in a Texas reservoir by introduced grass carp led to shift in community structure from a predominantly benthic to a pelagic based food web, and reported an associated decline in phytophilic fish abundance. In coastal rivers, the downstream transport of material and decreased water residence time compared to lentic ecosystems likely inhibited the production and biomass of plankton in the rivers, resulting in a decreased primary food base driven by filamentous algae production. Furthermore, the observed communities in coastal rivers are influenced by the colonization of marine fishes and invertebrates from the Gulf of Mexico and are not limited to within system recruitment compared to closed ecosystems. Therefore, community changes in the open coastal ecosystem cannot be predicted by in-stream processes alone, as demonstrated by the considerable differences between predicted and observed biomasses of marine fishes. The experimental removal of macroalgae in a coastal estuary resulted in a positive response in macrophyte, decapod and fish biomass (Deegan et al. 2002). Via a nitrogen tracer experiment, Deegan et al. (2002) demonstrated that macroalgae contributed little to secondary consumer production in the estuary. Their results support my conclusions that vegetative habitat loss results in decreased invertebrate and fish biomass, and indicate that production by filamentous algae may not compensate for the loss of macrophytes and associated periphyton in coastal aquatic ecosystems.

Coastal seagrass meadows are some of the most productive (Odum 1957) and ecologically valuable ecosystems in the world (Duarte 2002). Eutrophication and other human related disturbances to aquatic ecosystems have resulted in the global decline of seagrasses and other aquatic macrophytes (Short 1996, McGlathery 2001). The consequences of seagrass loss to the coastal faunal communities are not fully understood; although there is a general agreement that this habitat loss decreases biodiversity and biomass of fishes and invertebrates and alters food web structure (Nakamura 2010, Pillay et al. 2010, Coll et al. 2011). The results of this study corroborated those conclusions. In general, the loss of seagrass communities from coastal ecosystems is predicted to result in altered fish and invertebrate community structure and a decline in consumer biomass. Using the coastal river ecosystem as a model of community structure effects, the loss of macrophytes and shift to seasonal filamentous algae production was predicted to result in an overall 60% decrease in invertebrate biomass and 11% decrease in fish biomass, while restoration to historical biomass was predicted to result in an increase of 152% in invertebrate biomass and 75% increase in fish biomass. Since many developed and undeveloped nations depend on marine fisheries for food and revenue, the restoration of macrophyte communities is expected to have significant socioeconomic benefits through increased biomass of fishes and invertebrates that support coastal fisheries.

Future research that could increase the overall understanding of trophic dynamics in coastal ecosystems and likely improve the accuracy of ecosystem model predictions, include diet composition information for small-bodied fishes and invertebrates, annual production estimates of producers and invertebrates, and information on fish recruitment under variable vegetative habitat composition and biomass. Diet information of small-bodied fishes and invertebrates may provide greater insight into the transfer of energy from producers to predators. Since the scope of this study was limited to diet sampling of large-bodied fishes, there is considerable uncertainty in the contribution of each producer to the aquatic food web. Production estimates of producers and invertebrates that identify the proportion of primary production contributed by macrophytes, periphyton and filamentous algae could provide more accurate estimates of the effects of vegetation composition on secondary production. Finally, defining the relationship between vegetative habitat and fish recruitment would increase the ability to predict community responses to shifting habitat composition and biomass in coastal aquatic ecosystems.

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BIOGRAPHICAL SKETCH

Matthew Lauretta was born and raised in Phoenix, Arizona where he spent his youth exploring the desert, swimming and playing basketball. After graduating high school, he moved to Flagstaff to enjoy the college lifestyle at Northern Arizona University, located on the cool and mountainous Colorado Plateau. At NAU, Matthew studied environmental chemistry and worked as an undergraduate research technician for the Pinyon Ecology Research Group in the Department of Biological Sciences. He received two undergraduate research awards for his independent study on the use of stable nitrogen isotopes in predicting pinyon tree susceptibility to insect infestation. After graduation, he worked as a field technician monitoring insect, bird, reptile, amphibian and mammal populations along the Colorado River in Grand Canyon. That experience led to a great opportunity to study the native fishes in the Colorado River, including the endangered humpback chub (*Gila cypha*). Between the ages of 19 and 26, Matthew spent over 525 days sleeping under the stars while researching the Grand Canyon ecosystem. In addition, he was involved in fish monitoring and environmental assessment studies in several other rivers in Arizona and New Mexico including the Rio Grande, Pecos and Gila rivers. Matthew received his Ph.D. in fisheries and aquatic sciences from the University of Florida in December 2011, where his research focused on habitat loss effects to fish and invertebrate communities in Florida's coastal river ecosystems.