ABSTRACT

PINE, WILLIAM EARL, III. Population Ecology of Introduced Flathead Catfish. (Under the direction of Dr. Thomas J. Kwak and Dr. James A. Rice.)

Invasive aquatic species are becoming increasingly problematic for aquatic ecologists and resource managers, as the ecological and economic impacts of introductions become better known. The flathead catfish *Pylodictis olivaris* is a large piscivorous fish native to most of the interior basin of the United States. Via legal and illegal introductions, they have been introduced into at least 13 U.S. states and one Canadian province primarily along the Atlantic slope. I used a variety of capture-recapture models to estimate flathead catfish population parameters in three North Carolina coastal plain rivers (Contentnea Creek, Northeast Cape Fear River, and Lumber River). My estimates using a Jolly-Seber model were hindered by low capture probabilities and high temporary emigration. Reasonable estimates were possible using a robust-design framework to estimate population size and temporary emigration with supplemental information from a radio-telemetry study to examine model assumptions. Population size estimates using a robust design model including temporary emigration ranged from 4 to 31 fish/km (>125-mm total length, TL) of sampling reach. Additional analyses showed high rates of temporary emigration (>90%), independently supported by radio-telemetry results. I also examined flathead catfish diet in these rivers and found that flathead catfish fed on a wide variety of freshwater fish and invertebrates, anadromous fish, and occasionally estuarine fish and invertebrates. Fish or crayfish comprised more than 50% of the stomach contents by percent occurrence, percent-by-number, and percent-by-weight in all rivers and years. A significant difference in the diet composition percent-by-number was found between Contentnea Creek and the Northeast

Cape Fear River. Significant differences were not detected between years within Contentnea Creek but were found within the Northeast Cape Fear River. Feeding intensity (as measured by stomach fullness) was highest in the Northeast Cape Fear River associated with a lower mean size of feeding flathead catfish in this river than of those in Contentnea Creek or the Lumber River. A significant correlation between diet item length and flathead catfish total length was found for Contentnea Creek in 2001. This relationship was not significant in the Northeast Cape Fear River in either year. Based on the diet composition data collected in this study and those published on native and introduced flathead catfish populations, I am not able to support or refute the hypothesis that flathead catfish are preferentially feeding on specific species or families. However, the flathead catfish populations examined here are well established, and the greatest impact from selective predation may have occurred immediately following introduction. Based on my findings, flathead catfish could restructure or suppress native fish communities in coastal rivers through direct predation because of their primarily piscivorous food habits. To evaluate the potential ecosystem impact of this invasive species on the native fish community, I developed an ecosystem simulation model (including flathead catfish) based on empirical data collected for a North Carolina coastal river. Model results suggest that flathead catfish suppress native fish community biomass by 5-50% through both predatory and competitive interactions. However, these reductions could be mitigated through sustained exploitation of flathead catfish by recreational or commercial fishers at levels equivalent to those for native flathead catfish populations (6-25% annual exploitation). These findings demonstrate the potential for using directed harvest of an invasive species to mitigate the negative impacts to native species.

POPULATION ECOLOGY OF INTRODUCED FLATHEAD CATFISH

by

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BIOGRAPHY

I was born William (Bill) Earl Pine, III to Loye Zeanah Pine and William (Kip) Earl Pine, Jr. on 20 August 1975, in Grove Hill, Alabama. My academic and career path is an extension of childhood opportunities and experiences across the great state of Alabama. I began my fisheries education at Auburn University in the fall of 1993. My experiences at Auburn University were formative in shaping me into the person that I am now. An early mentor, Dr. Bill Davies, helped me to secure a position working with Dr. Dennis DeVries, in whose lab I remained during my four years at Auburn. It was through my work with the outstanding members of this lab that I developed the professional skills and friendships that have carried me through my Ph.D. Following graduation from Auburn in 1997, I began my M.S. degree with Dr. Mike Allen at the University of Florida. Dr. Allen was both generous in the learning and research opportunities he provided, and rigorous in his expectations of my performance. I thrived in this work environment and consider Mike to be one of my best professional and personal friends. Following graduation from the University of Florida in the fall of 1999, I was recruited by a long-time friend, Dr. Rich Noble, for the Ph.D. program in Zoology at North Carolina State University. I moved to Raleigh in the summer of 2000 and enrolled in the Zoology Department under the supervision of Drs. Tom Kwak and Jim Rice. My research on introduced riverine populations of flathead catfish has been the most challenging fisheries project with which I have been involved. I defended my dissertation in the fall of 2003, and I am now looking forward to the next learning opportunity.

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This project was a massive undertaking requiring careful planning and a large field effort. The name “Team Flathead” developed early and remains appropriate– this project was truly a team effort. I thank Scott Waters, NCSU Research Associate, for his efforts and participation in every aspect of the project. Drew Dutterer and Ed Malindzak provided good attitudes and outstanding technical support throughout long and difficult field days. Wendy Moore, NC Coop Unit Program Assistant provided tremendous logistical support. Christian Waters, Keith Ashley, Tom Rachels, Kent Nelson, Pete Kornegay, and Scott Van Horn from the NCWRC readily provided field assistance and technical insight throughout this project.

I owe tremendous thanks to my family, particularly my wife Julie. She has graciously and lovingly supported my learning efforts in every way asked. My parents recognized my early interest in science and have unwaveringly supported me. The cost of this support cannot be measured and simple thanks is not enough– I can assure you that I will do the same for my children in your honor. My brother David and sister Rebekah have always provided loving support and inspiration to me. I have a large extended family of

Aunts, Grandparents, and in-laws to which I am grateful. Knowing that your family supports you is a tremendous help in the often solo pursuit of knowledge.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Introduction and Justification

The introduction of non-native species is an ecologically significant, yet poorly understood component of anthropogenic aquatic habitat alteration. The impact of non-native species can be evaluated ecologically via functional or species changes within the introduced ecosystem or economically by cost estimates to mitigate ecosystem changes following species introduction. The purpose of this dissertation is to evaluate the ecological interactions between native fish communities and a non-native, piscivorous flathead catfish *Pylodictis olivaris*, in three coastal North Carolina rivers.

Flathead catfish are large predatory fish native to most river systems within the interior basin of the United States and now introduced along much of the mid-Atlantic slope and portions of the Pacific slope. Flathead catfish have currently established reproducing populations in at least 13 US States and one Canadian province (Jackson 1999). Flathead catfish have frequently been introduced as a recreational sportfish species because of their potential for large size, fighting ability when hooked, and palatable flesh. No ecologically similar native species exist within the introduced range. Following the introduction of flathead catfish, there have been corollary declines in a wide variety of native fish species including native catfishes and sunfishes. This has led to widespread concern that the establishment of flathead catfish may come at the expense of native fish diversity and inherent biological stability.

To study these interactions between native fish communities and flathead catfish, I estimated population size and sampled stomach contents of flathead catfish and determined native fish community composition and abundance in three coastal North Carolina rivers. I then linked this information for flathead catfish and native fish groups in a mass balance (Ecopath) model to examine energy transfer linkages between the native fish community and flathead catfish. Finally, I used the mass balance model to simulate changes in ecosystem structure following intensive harvest of flathead catfish at various exploitation rates. These findings were then compiled and presented as a potential impact scenario following flathead introduction and compared to the original flathead catfish introduction in North Carolina. Also, several potential management scenarios related to flathead catfish harvest as a tool to assist with native fish community restoration were evaluated.

This dissertation is presented as five manuscripts. Chapter Two is a review of capture-recapture methods for estimating population size. This chapter has been accepted for publication in *Fisheries* and is written in first-person plural tense to reflect the joint authorship among myself, Ken Pollock, Joe Hightower, Tom Kwak, and Jim Rice. Other chapters are written in first-person singular tense. Chapter Three is a capture-recapture study to estimate flathead catfish population size in each study river. Chapter Four is an analysis of the flathead catfish stomach content data. Chapter Five is a series of models which synthesize each of the above components and evaluate ecosystem response to flathead catfish introduction and harvest. Chapter Six discusses how these findings fit a set of empirically derived rules describing other invasive aquatic species and provides recommendations for future research related to introduced flathead catfish ecology.

CHAPTER 2

A REVIEW OF TAGGING METHODS FOR ESTIMATING FISH POPULATION SIZE AND COMPONENTS OF MORTALITY

Abstract

Techniques to improve estimation of animal population size and mortality from tagging studies have received substantial attention from terrestrial biologists and statisticians during the last 20 years. However, these techniques have received little notice from fisheries biologists, despite the widespread applicability to fisheries research, the wide variety of tag types used in fisheries research (from traditional fin clips to telemetry tags), and the development of new computer software to assist with analyses. We present a brief review of population models based on recaptures, returns, or telemetry relocations of tagged fish that can be used to estimate population size, total mortality, and components of mortality (i.e., fishing and natural) that are frequently of interest to fisheries biologists. Recommended strategies include (1) use closed population models (e.g., Lincoln-Petersen) to estimate population size for short term studies where closure assumption can be met, (2) use the robust design to estimate population size for studies of longer duration, (3) use high-reward tags in conjunction with other methods of estimating reporting rate in tag-return studies, (4) combine a subset of telemetry tagged fish with either a high-reward tagging program or a traditional capture-recapture study to improve mortality estimates and understanding of mortality components, and (5) use pilot studies and simulation analyses to assess precision of estimated parameters to evaluate study feasibility. Incorporation of these improved techniques could lead to greater accuracy and precision of parameter estimates from tagging studies and thus to improved understanding and management of fish populations.

Introduction

Effective fisheries management often requires reliable information on population size, survival, and mortality. For example, the population size of imperiled fish species is often a critical factor in determining its protected status, and recovery plans often focus on ways to increase species abundance by understanding mortality components and reducing mortality rates (Pine et al. 2001). Management actions such as the evaluation of marine protection areas also frequently use indices of animal abundance to assess the effectiveness of restrictions on fishing mortality (Russ and Alcala 1996). Fish stocks with commercial and recreational value are usually managed with a goal of maintaining sustainable harvests through regulation of fishing mortality (Hilborn and Walters 1992).

Capture-recapture methods with tagged animals are a primary means of estimating the abundance and survival of animal populations. These methods have received considerable attention over the last century from wildlife biologists and statisticians interested in developing applied statistical models to estimate animal abundance (Pollock 1991; Williams et al. 2002). Tag-return methods are also a primary means of estimating a population's total mortality rate, and in some fisheries settings, the natural and fishing components of mortality (Brownie et al. 1985; Hoenig et al. 1998a; Pollock et al. 2001a). Such tag return models are basically special extensions of capture-recapture models used to estimate population size, survival rates, and recruitment (i.e., "Jolly-Seber" models, Seber 1982). The key difference is, for a capture-recapture model, the biologist conducts the sampling at specific points in time to recapture tagged fish alive. For application of a tag-return model, returns of harvested fish come from one or more fisheries over an extended period of time (e.g., fishing season).

It is our observation that fisheries biologists have been less aggressive in adopting these models for estimating population size, survival rates, and mortality rates, relative to our wildlife counterparts. This may be due to unfamiliarity with the methods or software as well as practical concerns. We also have observed that tagging studies to estimate population size and survival rates (e.g., Jolly-Seber) are frequently considered separately from tagging studies used to estimate mortality rates (e.g., Brownie models). Information from both study types is useful to fisheries managers, and the purpose of this article is to review tagging methods for estimating population size and mortality components for fisheries applications. Our review is intended to assist fisheries biologists in designing tagging studies by summarizing the underlying assumptions and basic models available within the framework of available specialized software (Box 1, Tables 1 and 2). Our hope is that this review will encourage fisheries biologists to utilize these techniques in their research efforts.

Capture-recapture versus Catch-per-unit-effort

Catch-per-unit-effort (CPUE) data are often used as a relative index of population size. However, this approach assumes that catchability or probability of capture is consistent over time. The relationship between catch rate and actual abundance is not generally considered, and it is unlikely that capture probability will be constant over time and under varying sampling conditions (Williams et al. 2002). That relationship is important, because fish sampling techniques rarely collect all animals present in an area and fish behaviors (e.g., schooling) may concentrate fish such that catches remain high, even if populations are declining (Hilborn and Walters 1992). Capture-recapture models provide direct estimates of both population size and the probability of capturing an individual while CPUE only demonstrates trends in catches which may (or may not) be related to population abundance (Williams et al. 2002). In general, if the primary study objective is to detect large (e.g., >50%) changes in population abundance, then CPUE data may be adequate. In situations where more precise information on population size and trends, or information on mortality and its components are of interest, then a tagging study is likely the best approach.

The two approaches can be compared by considering the common situation of sampling largemouth bass (*Micropterus salmoides*) in reservoirs with shoreline electrofishing transects. Due to gear avoidance or sampling difficulties related to physical structure, it is unlikely that every largemouth bass along the shoreline is collected. Instead, we can conceptualize a model where each fish will have a capture probability (p_i), which can then be used to estimate the number of largemouth bass in the transect ($\hat{N}_i$) from the number of fish collected in the sample (C_i), where

$$\hat{N}_i = \frac{C_i}{p_i} \quad . \tag{1}$$

The capture probability, p_i , is the probability of a fish being caught at that time (*i)* and location with the gear employed. The use of estimates of capture probability ($\hat{p}$) to account for individuals that are not collected in an area is critical to generating precise and accurate estimates of population size.

Because capture probability is rarely constant, it is not possible to separate changes in p_i from changes in population size if CPUE is considered alone (Pollock et al. 2002;

Williams et al. 2002). Returning to our example, if an electrofishing sample collected along the same transect six months later included only 10% of the number of fish caught in the previous transect, is this because fewer fish are present along the shoreline, or has the p_i changed because of a change in water temperature, vegetative cover, or some other environmental factor? Bayley and Austen (2002) demonstrated wide variation in the catchability of lentic fishes across a range of fish species, fish size, and varying environmental conditions. This is not surprising to field biologists who routinely notice changes in catch rate with changes in environmental conditions (e.g., weather) or seasonal patterns in recruitment and movement.

A key parameter in a capture-recapture study is the capture probability, which can be defined as the probability that an individual animal is captured on a sampling occasion. In practical terms, it can also be thought of as the fraction of the study population captured on that occasion. It is generally estimated from the recapture of tagged individuals, and should be as high as possible in order to obtain reliable estimates of population parameters. Unfortunately, the literature and our own experiences in conducting these types of studies have shown that capture probability is low in most fisheries studies, resulting in "sparse" data. The typically low efficiency of fisheries sampling methods is illustrated by Bayley and Austen (2002). They sampled known populations of various species in reservoirs and ponds and reported empirical estimates of catchability (the fraction of fish collected in a single pass in an electrofishing boat) that ranged from 2 –14%.

Tagging studies require that fish that are collected, tagged, and released be in good condition and as likely to be captured (or harvested) as untagged fish in a future sample.

This compels biologists to use non-lethal collection techniques that may not be the most efficient gears available. Collection restrictions placed on researchers by permitting agencies may also limit the use of some techniques or sampling programs (e.g., placing limits on gillnet soak time or electrofishing settings), particularly with imperiled species (Pine et al. 2001; Holliman et al. 2003). Because capture probability drives accuracy and precision of parameter estimates, biologists should design their sampling programs to maximize capture probability.

<u>Capture-recapture models</u>

One approach to estimating capture probability and population size is to use capture-recapture (mark-recapture) methods. These methods have been intensively studied by biostatisticians and applied widely to terrestrial wildlife populations (Lancia et al. 1994; Williams et al. 2002). In these studies, fish are recaptured alive on multiple occasions, unlike tag-return studies (described below) where there is only one "recapture" in the harvest - and the fish is dead.

Capture-recapture models can be broadly defined as open or closed population models, each with specific assumptions. Closed population models are "closed" to changes in the population due to births, deaths, emigration, or immigration, whereas open models allow for these changes. Both closed and open models estimate capture probability and population size. In addition, open models are able to estimate apparent survival, recruitment, and population change. Detailed explanations and examples of each are discussed below.

Closed Models

Models that assume equal catchability among individuals and sample dates, such as Lincoln-Petersen and Schnabel models (Figure 1), have a long history of use in fisheries applications (Ricker 1975). These models have strict assumptions that are frequently violated to varying degrees, which results in biased population estimates. The basic Lincoln-Petersen model is based on a sample of n_1 animals caught, marked with individual (e.g., PIT tag) or batch marks (e.g., fin clip), and released at time one. A second sample n_2, is then taken at time two and the number of marked animals m_2 is noted. The equation for the population estimate (Ricker 1975) is

$$\hat{N} = \frac{n_1 n_2}{m_2}. \tag{2}$$

The rationale for this model is that the fraction of marked fish in the second sample ($\frac{m_2}{n_2}$), should on average equal the fraction of the population that is marked ($\frac{n_1}{N}$).

The widely used "Schnabel" model (Ricker 1975) is basically an extension of the Lincoln-Petersen model that allows for more than two samples with a batch mark. The assumptions for both models are that (1) the population is closed to additions (recruitment or immigration) or deletions (deaths or emigration), (2) capture probability is equal among all animals in each sample, and (3) marks are not lost or overlooked.

In capture-recapture studies lasting longer than a few days, the closed model assumption of no additions or deletions occurring in the population may be unrealistic. Although recruitment and mortality may be negligible or low for a species over a period of time longer than a few days (perhaps even a season), movement into or out of the study area often precludes the use of closed population models. A variety of studies have revealed movement patterns in adult and juvenile fishes that would violate the closure assumption (e.g., Cleary and Greenbank 1954; Skalski and Gilliam 2000; Hightower et al. 2001; Mitro and Zale 2002).

Heterogeneity in capture probability may be an important source of bias if traditional Lincoln-Petersen and Schnabel models are used. Heterogeneity can be related to differences in fish size, sex, or social status (assumption 2, equal catchability). Many fisheries gears are strongly size selective. For example, electrofishing is known to select for larger individuals (Reynolds 1996), which likely leads to electrofishing samples containing disproportionate numbers of large individuals relative to their actual abundance. Lincoln-Petersen and Schnabel models do not account for such heterogeneity (which leads to strong negative bias in population size). Estimates may be produced separately for important strata, (size, sex, or status), to minimize heterogeneity within a stratum (Kwak 1992), but this approach results in reduced sample sizes for each estimate and corresponding reduced precision. Program SPAS can be used to analyze 2-sample capture-recapture data over several strata to account for heterogeneity provided sufficient recaptures are collected within each strata (Table 1).

An additional source of variation in capture probability is “trap response” or behavior, where capture probability depends on an animal’s previous capture experience. An animal may be less or more likely to be caught in future samples because it has learned to avoid, or is attracted to, a trap. For example, fish behavior was shown to be altered for at least 24 h following electrofishing and marking (Mesa and Schreck 1989).

Tag loss is common in fisheries studies (Guy et al. 1996, violation of assumption 3) and can result in very serious bias in $\hat{N}$. Tag loss can be estimated by double tagging some individuals (Guy et al. 1996) and then adjusting the number of recaptures to account for this loss. For this approach, tag loss must be assumed to be independent for the two tags. If possible, tag type and location should be evaluated with a pilot study to ensure that tag retention will be adequate, and provide the researcher with experience in tagging procedures.

The Lincoln-Petersen and Schnabel models are widely used in fisheries applications because they are easily implemented, computationally simple, and most importantly, individual fish do not have to be uniquely marked. Despite these advantages, we recommend applying individual marks to obtain the complete capture history of each fish, so that the degree of heterogeneity and trap response in capture probabilities may be assessed and accounted for. Capture histories are often recorded as a series of 1s and 0s, where 1 indicates an animal was caught in that sampling period, and 0 indicates the animal was not caught. This method of recording capture histories of individual animals is the standard means of entering data into capture-recapture software packages.

A suite of eight closed models has been developed to allow for variation in capture probability related to physical, behavioral, and temporal attributes of the study species or sampling design (Otis et al. 1978). These models are available in program CAPTURE, a computer software program designed to assist with analyzing capture-recapture data available at no cost through the World Wide Web as a stand alone program or accessed through another free software program, MARK, discussed later (Table 1). Model M_o is the simplest model for closed populations and does not allow for changes in capture probability due to heterogeneity, behavior, or time (Pollock et al. 1990; Lancia et al. 1994). The heterogeneity model (M_h) allows each animal to have a unique capture probability (due to size, sex, etc.) but this capture probability must remain constant among all sampling periods i. The trap response/behavior model M_b estimates an initial capture probability $\hat{p}$ and recapture probability ($\hat{c}$), which may differ from each other. Model M_t allows capture probability to vary among sampling periods, but it must remain constant among individuals for each period. This model is the same as the Schnabel model. Models M_{tb}, M_{bh}, M_{th}, and M_{tbh} are combinations of the above, but require additional assumptions (for more detail see Norris and Pollock 1995; Pledger 2000; Williams et al. 2002). Program CAPTURE is the only specialized program available that can be used to fit each of these heterogeneity models to capture histories from a capture-recapture study. Program CAPTURE also uses a model selection approach based on a large number of goodness-of-fit tests to assist with choosing the model that best fits the data. However, the model selection routine in CAPTURE does not perform well with sparse data; thus, biologists should evaluate models closely in terms of meeting assumptions to select the simplest model that best describes the data (Pollock et al. 1990; Williams et al. 2002).

The Schnabel model is simple in design and analysis and has been widely used in fisheries applications (Ricker 1975; McInerny and Cross 1999; Kocovsky and Carline 2001). Capture probability can vary among sampling periods with this model (analogous to model M_t in CAPTURE). Although the Schnabel model is computationally simple (Table 2, no need for computer analysis), we suggest using program CAPTURE for analyzing such data because CAPTURE can fit and evaluate several models in addition to the Schnabel model.

For example, CAPTURE can compare the M_t (Schnabel) model, which does not allow for heterogeneity, with the M_{th} model, which allows for varying capture probabilities among individuals (heterogeneity) and among sampling occasions. The M_{th} model may be more realistic because it accounts for heterogeneity, whereas the M_t is highly biased by unequal capture probabilities (heterogeneity) within each time period (Lancia et al. 1994). We consider heterogeneity in capture probability to be present in almost all fisheries applications and suggest that the Schnabel model (M_t in CAPTURE) be used only if it is chosen by a model selection procedure. However, in samples with extremely low capture probability (<0.05), M_t (or the similar Chao M_t model also available in CAPTURE, Chao 1989) may be the only model that CAPTURE is able to fit to the data for a population estimate (Mitro and Zale 2002). In this case, estimates should be evaluated in terms of the severity of potential assumption violations, particularly that for heterogeneity.

Removal Studies

Depletion or removal studies are widely used in fisheries applications and are analogous to closed capture-recapture model M_b in CAPTURE (Ricker 1975; Otis et al. 1978). M_b allows for animals that have been captured previously to demonstrate a different capture probability than those that have not been captured. This “trap response” is mathematically analogous to a removal model because only initial captures of animals are used in estimating population size (Pollock et al.1990). Model M_b assumes that the initial capture probability is constant among animals. Model M_{bh} as applied to removal studies relaxes that equal catchability assumption by allowing individual animals to have different removal probabilities between animals but requires that the removal probability does not change over time.

Similar to closed models, accurate population size estimates from removal studies rely on minimally adequate capture probabilities and initial population size. White et al. (1982) recommended capture probabilities of 0.2 and population sizes of 200 individuals based on simulation studies for reliable population size estimates. There is also the question of the number of samples. We recommend removal studies that incorporate four or more samples to allow the possibility of accounting for heterogeneity among individuals.

CAPTURE's maximum-likelihood estimation of *N* generates similar estimates to those of the regression technique commonly used in removal studies (Lancia et al. 1994). A disadvantage of the regression approach is the potential for violating assumptions required for linear regression, such as homogenous variances among regressed points (Pollock 1991). Because of this and other potential violations, the wider range of models available, and model selection assistance provided in program CAPTURE, we re-emphasize the recommendation of Lancia et al. (1994) and Pollock (1991) to use CAPTURE for removal studies.

Design of short-term studies

Biologists estimating population size should carefully consider designing their study to meet the assumptions of the closed population models available in CAPTURE. Sampling areas that cannot be closed physically might be treated as closed over short time periods (Pollock 1982), as did Osmundson and Burnham (1998) for Colorado squawfish (*Ptychocheilus lucius*) and Mitro and Zale (2002) for rainbow trout (*Oncorhynchus mykiss*).

However, we strongly recommend that emigration be closely examined by either searching for tagged fish outside of the sample reach or through the use of a subset of radio-tagged individuals (e.g., Zehfuss et al. 1999).

Mitro and Zale (2002) used a pilot study and computer simulation to evaluate the precision of population size estimates using the closed models in CAPTURE before conducting the major field component of their study. We encourage careful study planning (Box 1) to help evaluate precision of population parameter estimates prior to conducting a large field study. We also believe that M_h or M_{th} often will be the most realistic models to fit in fisheries applications. Closed models are less complex (fewer parameters) than open population models and are reasonable approaches for sparse data. We caution that population estimates from closed models should be closely evaluated in terms of sensitivity to model assumptions.

Open Population Capture-Recapture Models

The Jolly-Seber model (Jolly 1965; Seber 1965) and its variations (Cormack 1964; Pollock et al. 1990; Williams et al. 2002) are the primary open population capture-recapture models suitable for fisheries applications. Three computer programs, JOLLY (Pollock et al. 1990), MARK (White and Burnham 1999), and POPAN (Aarnason and Schwarz 1999), are capable of analyzing capture-recapture data from open populations (Table 2). These programs are also available at no cost through the World Wide Web (Table 1). The Jolly-Seber model allows population size estimation at each sampling date (excluding the first and last), estimation of apparent survival between samples, and the addition of new recruits between samples. Survival rates and recruitment numbers apply to the pool from which marked animals are sampled. For example, if tagged individuals are adults, then recruits into this population are juveniles entering the pool of tagged adult fish and not new individuals being born into the population. The "survival" estimated here actually is apparent survival (Φ = 1-mortality-emigration); for apparent survival to be true survival (*S*), emigration must not occur (Pollock et al. 1990). It is not possible to estimate true survival and emigration separately unless one collects additional data on emigration. For example, a telemetry study could be simultaneously conducted with the tagging study to help determine the rate and extent of emigration from the study site. The differences between true and apparent survival should be considered when comparing survival estimates from capture-recapture studies with traditional fisheries estimates (e.g., catch-curves Fabrizio et al. 1997).

The Jolly-Seber model assumes the following: (1) every animal present in the population at sampling time *i* has an equal probability of capture, (2) survival is equal for every marked animal that is present from one sampling period to the next, (3) tags or marks are not overlooked or lost, (4) all animals are released immediately after the sample and all sample periods have a short duration (i.e., instantaneous) (Seber 1982). Violation of the equal catchability (no heterogeneity) assumption (number one above) will overestimate the actual proportion of marked animals in the population and lead to a negative bias in population size (Pollock et al. 1990). Negative bias in the estimated survival rate occurs when survival is affected by the tag or tagging procedure (assumption 2 above) (Arnason and Mills 1981). In fisheries applications, tagging trauma may cause lower survival for newly tagged fish. Models have been developed to detect this initial decrease in survival and adjust estimates accordingly (Brownie and Robson 1983). Tag loss can lead to serious underestimation of survival rates and overestimation of population size by decreasing the number of recaptures in the population. Double-tagging experiments can help estimate and adjust for tag loss (Arnason and Mills 1981).

An assumption of the Jolly-Seber model is that all emigration is permanent. Natural movement patterns of the study animal can lead to "temporary" emigration, where the animal is entering and leaving the study site repeatedly. There are two types of temporary emigration, "Markovian" emigration where an animal "remembers" that it has left the study area and returns based on some time-dependent function, and "random" emigration where the animal randomly leaves and returns on a continual basis (Kendall et al. 1997). The presence of a Markovian emigrant in a sample depends on the location of the animal in the previous sampling period (i.e., was the animal available for capture in the sampled area?), whereas a random emigrant does not depend on its location in the previous sample period. Temporary emigration may occur in some fisheries studies, resulting in biased survival and population size estimates. Zehfuss et al. (1999) showed that unbiased estimates of N could be obtained from Jolly-Seber models, even with random temporary emigration, if capture probabilities remained high ($\hat{p}_i$ >0.5, unlikely in most field applications). However, in situations with low $\hat{p}_i$ values and Markovian temporary emigration, estimates of N can be negatively biased (Zehfuss et al. 1999).

Several fisheries examples of Jolly-Seber model applications for imperiled fish species appear in the literature. Douglas and Marsh (1998) used Jolly-Seber and Cormack-Jolly-Seber models (which emphasize survival estimation, Cormack 1964) to estimate population size and survival for rare catostomids in the Little Colorado River over a four-year period. Fabrizio et al. (1997) estimated survival of a recovering lake trout (*Salvelinus namaycush*) population using Jolly-Seber and catch-curve methods in Lake Michigan. They found similar estimates for survival between the two methods. Jolly-Seber models have also been successfully applied in several studies of Gulf of Mexico sturgeon (*Acipenser oxyrinchus desoti*) to estimate population size, population growth, and survival (Chapman et al. 1997; Zehfuss et al. 1999; Pine et al. 2001).

Robust Design Models

There are several major distinctions between closed and open models that we should now reiterate. Closed models are more likely to provide useful estimates from sparse data than open models. Closed models are also able to account for heterogeneity in capture probability and trap response. However, the "closure" assumption of these models generally restricts their applicability to short-term studies (i.e., < 1-month, Table 2). Open models such as the Jolly-Seber model are appealing because they are "open" to population changes due to movement, mortality, and recruitment. The difficulty in applying open models is that there are many parameters to be estimated, so these models perform poorly with sparse data. Pollock (1982) presented a sampling design that combines the strengths of both closed and open models and has widespread potential use in fisheries studies. This "robust design" is a series of short-term closed population studies (which allow for heterogeneity and trap response in capture probability) linked by open population models (which are used to estimate survival). This design allows population size to be estimated during the short-term studies (with closed population models) and survival and recruitment to be estimated with a Jolly-Seber model for the intervals between the closed periods (Figure 2). Versions of the robust design model in MARK allow for random or Markovian temporary emigration (Kendall et al. 1997).

The robust design approach performs well for fisheries studies composed of a series of short-term samples (secondary sampling periods) clustered within primary sampling periods that occur at longer time intervals. For example, a typical robust-design study would be a series of short-term population studies where fish are collected three times per week (noted l_1-l_3), once per month, over a four-month sampling season (K_1-K_4). During the "closed" portion of the study (three samples within a week), the closed population models in CAPTURE or MARK would be used to estimate population size for each of the one-week samples. We would then use a Jolly-Seber open model (in JOLLY or MARK) to estimate survival between each of the primary periods (Figure 2).

Incorporation of additional information

Another improvement on a standard capture-recapture study would be the use of auxiliary information. For example, capture probabilities could be estimated empirically by using known numbers of a species in the sampling area (e.g., radio-tagged individuals present) or using a model to predict catchability for a sampling gear given various species, habitats, and environmental conditions (Bayley and Austen 2002). These empirical estimates can then be compared to capture-probability estimates from capture-recapture studies. Individual covariates (e.g., fish length) can also be used to help reduce bias due to capture heterogeneity (Pollock 2002). The use of individual covariates is also appealing to biologists because it allows study of the relationship between the covariate and independent model parameters such as survival. These covariates can be fit in program MARK.

Model Selection

One useful approach for evaluating estimates from a capture-recapture study is to compare results of several different models used to analyze the same data set. The different estimates of population size can be evaluated in part by examining how well the assumptions for each model are met and how well each model fits the data. MARK evaluates how well each model fits the data using Akaike's Information Criterion (Akaike 1973; White and Burnham 2002; Burnham and Anderson 2002), which in many cases is a better model selection approach than the goodness-of-fit tests used in CAPTURE. For the typical fisheries situation with limited data, we recommend using the model selection criteria in conjunction with the biologist's knowledge of the system to select the most biologically meaningful and parsimonious model.

Tag return models

Tag-return models use harvest of previously tagged fish to estimate total mortality or survival rate (*S*) and tag-recovery rates (*f*). For a multi-year tag-return study, these "Brownie" models (Brownie et al. 1985) are the standard method of analyzing wildlife tag-return data (Williams et al. 2002) and can be widely applied in fisheries settings (Youngs and Robson 1975; Hoenig et al. 1998 a, b).

Many of the assumptions for tag-return models are the same as capture-recapture models, namely that the tagged fish sample is representative of the target population, tags are not lost, survival rates are not affected by tagging, and the fates of each tagged fish are independent. In addition, tag-return models assume (1) the year of the tag recoveries is correctly reported, (2) all tagged fish within a cohort have the same annual survival and recovery rates, and (3) fishing and natural mortality are additive.

In this type of study, annual cohorts of fish are tagged in different years, and then the tags from harvested fish (commercially or recreationally) are collected from fishers over a period of years. These tag returns are then used to estimate mortality parameters. Assuming that the individual cohorts are independent, then the overall likelihood function for the model is the product of each of the individual cohort likelihoods (Brownie et al. 1985). Programs MARK and SURVIV can be used to generate mortality estimates for multiple groups (ages, sexes) and examine dependence in S and f. Although an estimate of survival can theoretically be obtained from only two years of tagging and recovery, in practice at least three and preferably five years are needed (Brownie et al. 1985; Wiliams et al. 2002). The number of fish tagged each year will depend on the tag-recovery rate and desired precision, and can be explored using the methods outlined in Box 1. Brownie et al. (1985) suggest that tagging 300 individuals per year is a useful minimum sample size in order to obtain reliable estimates of survival for waterfowl.

By combining total mortality estimates from a Brownie model with information about the tag-reporting rate, mortality can be partitioned into fishing and natural-mortality rates (Pollock et al. 1991; Hoenig et al. 1998 a, b). The tag-return rate f is defined as

$$f = \lambda u, \tag{3}$$

where λ is the probability that a tag on a harvested fish is reported, and u is the exploitation rate. If λ, can be estimated, then and estimate of the exploitation rate u can be solved for.

To separate components of mortality, we do not need to assume that all tags are reported (Table 2), but we require an estimate of the tag-reporting rate. Methods for estimating reporting rate vary widely and include relying on surreptitiously planted tags, angler or port surveys, high-reward tags, or catch information from multi-component fisheries. These methods are reviewed in Pollock et al. (2001a), and each has their own assumptions that may be difficult to meet. Exploitation rates should be examined across a range of possible reporting rates to assess how errors in reporting rate influence the estimates of exploitation and alter possible management strategies.

One common method of estimating tag reporting rate in wildlife and fisheries studies is to use two tag types, standard tags and high-reward tags, and assume 100% reporting rate for the high-reward tags (Henny and Burnham 1976; Conroy and Blandin 1984; Pollock et al. 1991). The standard tag-return rate can then be estimated as the relative recovery rate of standard tags to the recovery rate of the high-reward tags. If high-reward tags are not 100% reported, then the standard tag-reporting rate is positively biased (Pollock et al. 2001a). Angler behavior may also change as a result of the high reward tags. Anglers may report regular tags at a higher rate due to publicity associated with the high-reward tags. Pollock et al. (2001a) recommended that reward tags be used every year of tagging so that angler behavior is not altered. Although this may increase the cost of the tagging program, the tradeoff of having more accurate estimates may justify the higher cost. Denson et al. (2002) used the high reward tagging method and estimated the reporting rate for red drum (*Sciaenops ocellatus*) was approximately 60%.

Exploitation rate (u) can also be estimated from a single release of tagged fish, based on the fraction of tags that are returned from harvested individuals. The most important assumption of this method is that all recovered tags are reported, or that a precise external estimate of the reporting rate is available (see above). For the typical fishery in which fishing mortality (F) and natural mortality (M) are operating concurrently, the exploitation rate is defined as

$$u = \frac{F\left(1 - \exp^{(-F-M)}\right)}{Z}. \tag{4}$$

Because the instantaneous total mortality rate (Z) is defined as $F + M$, the only two unknowns in this equation are F and M. If an estimate or (more likely) an assumed value of M is available, the estimate of u from a tagging study can be used to calculate an estimate of Z. Alternatively, if Z had been estimated externally (e.g., through a catch-curve analysis), then the equation can be solved for F and M. In situations where catch-curves cannot reliably estimate Z, the multi-year approach (above) would be required to obtain direct estimates of total mortality. Henry (2002) conducted an annual tagging program on Rodman Reservoir, Florida, to estimate tournament exploitation rate for largemouth bass. Variable reward tags of US \$5 to \$100 were used to estimate the reporting rate and F, a catch-curve was used to estimate Z, and then equation 4 was solved for M.

Telemetry methods

Telemetry methods have been widely used to estimate survival rates in terrestrial systems (White and Garrott 1990). They are becoming important in aquatic systems as well, largely because of improvements in transmitter and receiver technology that have increased reliability and dramatically decreased cost (see Voegeli et al. 2001). For example, remote sonic receivers are now available that allow continuous automatic monitoring of an area for several months and operate simply on one lithium cell battery (e.g., Heupel and Simpfendorfer 2002).

Transmitter characteristics that are important for mortality studies include (1) small size for implantation with no effect on the fish, allowing full recovery from capture and handling; (2) relatively long battery life; (3) adequate detection range, so that relocation probability is high; and (4) unique signal so that individuals can be distinguished.

The approach is to release a sample of telemetered animals, then locate each individual until it dies or is censored (e.g., excluded from the study because the animal is harvested, leaves the study area, or transmitter battery life is exceeded). An important difference between aquatic and terrestrial studies is that it is not generally possible to observe telemetered fish, so viability of the fish is inferred from movement between relocations.

Skalski et al. (2001) used radio telemetry to estimate survival rates of outmigrating salmon smolts in the Columbia River. They released radio-tagged smolts between successive dams and used automated receivers to estimate the fraction of fish that survived and passed each dam. Similar to the multiyear tagging approach, the ratio of detected transmitters from successive upstream release sites was an estimate of the survival rate because the "older" group of tagged fish would have passed one additional dam.

Telemetry methods are also effective for estimating components of the total mortality rate, including non-harvest rate (Hightower et al. 2001). An important advantage of this approach is that information about the tag reporting rate is not required. Also, unlike traditional tagging studies that provide information only through return of tags from harvested fish, telemetry studies can provide direct information about natural mortalities as well as fish that are alive (and moving between relocations).

The information that can be gained about sources of mortality depends on the study site and organism. Direct information about natural mortality can sometimes be obtained from telemetered fish that stop moving, whereas fishing mortality may be detected indirectly through the disappearance of telemetered fish from the study area (Hightower et al. 2001; Heupel and Simpfendorfer 2002). Natural mortality can also be detected from an atypical movement pattern or change in signal strength. For example, Jepsen et al. (1998, 2000) detected predation on radio-tagged Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) smolts by a decrease in transmitter signal strength (after telemetered smolts were eaten by northern pike [*Esox lucius*] or pikeperch [*Stizostedion lucioperca*]) or by tracking a transmitter into shallow water typically occupied by pike. Jepsen et al. (1998, 2000) confirmed that predation had occurred by electrofishing to capture pike and pikeperch with ingested transmitters. Predation by birds was established by tracking birds with ingested transmitters, locating a transmitter at an avian colony, or by disappearance of transmitters from the study area. Heupel and Simpfendorfer (2002) used an array of automated monitors to maintain continuous contact with telemetered juvenile blacktip sharks (*Carcharhinus limbatus*) in a nursery area. They inferred predation by a larger shark on two telemetered juveniles, based on the change in swimming speed and the location of both juveniles at exactly the same (moving) position.

Unlike traditional tagging studies, telemetry methods can also provide detailed information about the timing and spatial location of mortalities. For example, Jepsen et al.

(1998) conducted daily searches for radio-tagged salmonid smolts and established that predation mortality was concentrated in several areas, including a narrow constriction where a bridge crossed the reservoir. Heupel and Simpfendorfer (2002) monitored juvenile blacktip sharks during their first six months of life and established that natural and fishing mortality were concentrated within the first 12-15 weeks. Waters (1999) used telemetry methods to document that largemouth bass natural mortality varied seasonally in concert with seasonal patterns of spawning activity. Hightower et al. (2001) showed that natural mortality of striped bass (*Morone saxatilis*) was restricted to periods in summer and fall when suitable habitat was lacking.

Combined tagging-telemetry methods

A new approach that has considerable promise for estimating mortality rate is a combination of the tag-return and telemetry methods (Pollock et al., In Press). The tag-return method can be based on a large sample of fish, because tags are inexpensive, and it provides direct information about harvest from returned tags. The telemetry method is restricted to a small sample size (because transmitters are expensive) and is more labor-intensive, but provides direct information about natural mortality and does not require an estimate of the reporting rate. In simulation studies based on an annual sample size of 500 conventional tags and 50 transmitters, Pollock et al. (In Press) demonstrated that the combined method draws on the strengths of both and results in improved estimates of fishing and natural mortality rates, as well as an estimate of the reporting rate. For this combined method, estimates of M are best when F is low, but estimates of the reporting rate are best when F is high. Telemetry and capture-recapture models can also be combined to improve the precision of survival and emigration estimates (Nasution et al. 2001, 2002).

Conclusions

We emphasize the use of pilot and simulation studies prior to conducting a large-scale field study to help evaluate precision of parameter estimates. As described in Box 1, this can provide a good indication of whether study objectives can be met with the available sampling resources, and will establish realistic expectations for study results.

In planning a closed capture-recapture study, the assumption of closure should be carefully evaluated through preliminary field studies if possible. Careful consideration should be granted to heterogeneity models (M_h and M_{th}), given that heterogeneity in capture probability is likely in fisheries sampling and can lead to strong negative bias in population size estimates. Five or more sampling periods are recommended for any closed capture-recapture experiment, particularly if heterogeneity models are to be used.

In planning an open capture-recapture study, temporary emigration should be evaluated because it can lead to large biases in parameter estimates. Apparent survival estimates from Jolly-Seber models are not highly biased by heterogeneity, so that is less of an issue here than for closed models. If the capture-recapture experiment will be longer-term (e.g., > 1-month), the assumptions of an, open population model are more likely to be met than those of closed models. Temporary emigration can be assessed with a sub-set of telemetry tagged animals.

We strongly encourage the use of the robust capture-recapture design because (1) both heterogeneity and temporary emigration can be accounted for, resulting in less biased estimates of population parameters, (2) it utilizes strengths of both closed and open population models, and (3) design is simple and easily incorporated into many standard fisheries sampling programs.

Key points related to tagging studies to estimate mortality include (1) information on reporting rate is not required if total mortality is the primary parameter of interest, and (2) if total mortality is partitioned into F and M then reporting rate must be estimated (e.g., reward tagging). Important aspects of telemetry methods of estimating mortality are (1) uncertainty associated with relocations of telemetered fish can be minimized by conducting multiple searches over short time intervals to locate every tagged fish or by combining searches with remote receivers to assist with documenting location (or absence) of tagged fish, (2) an estimate of the reporting rate is not required in order to partition total mortality into F and M, (3) researchers should attempt to account for emigration and hooking mortality (sources of positive bias for F and M, respectively), and (4) combining multiple methods such as tagging with telemetry studies should be considered to improve mortality estimates and provide a complete assessment of mortality components.

We hope that this review will encourage fisheries biologists to consider making broader use of the wide array of tagging models available. We covered only a few of the principal approaches to estimating population parameters from tagging data. The design, implementation, and analysis of tagging studies are a dynamic field that exists at the interface between management and applied statistics. Both of these fields can benefit via increased communication between the two groups of scientists to better define the needs of management biologist and increase the application of the statistical modeler's efforts.

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Table 1. Product name, description, and World Wide Web address for various software packages to assist with analyzing data from tagging studies.

Product name	Description	World Wide Web address
MARK	Comprehensive program for most types of capture-recapture analysis including open, closed, and robust design models. Capture probability and survival directly estimated for open, closed, and robust models and population size estimation for closed and robust models.	http://www.cnr.colostate.edu/~gwhite/mark/mark.htm
CAPTURE	One of the first programs for estimating population size and capture probability in closed populations. Calculates estimates using a variety of models which are able to account for heterogeneity, behavioral response, time variation, in capture probability. Only software that contains heterogeneity models. Can be run as an option within MARK.	http://www.mbr-pwrc.usgs.gov/software
JOLLY	Program for estimating population size, survival, and capture probability of open populations.	http://www.mbr-pwrc.usgs.gov/software
SURVIV	Program used to calculate survival rates from user-specified survival functions including tag-return models. Not very user-friendly.	http://www.mbr-pwrc.usgs.gov/software
POPAN	Program for estimating population size and number of new recruits in open populations.	http://www.cs.umanitoba.ca/~popan/
SPAS	Program for estimating population size in stratified two-sample capture-recapture studies.	http://www.cs.umanitoba.ca/~popan/

Table 2. Model, type of mark required (batch or individual), source of fish used in study (research collection or fishery dependent), typical study duration, reporting rate requirement, key parameters, additional information generated, and principal software for estimating population size and mortality components from tagging models discussed in this review.

Model name	Type of mark required	Source of fish	Typical study duration	Reporting rate required?	Key demographic parameters	Additional information generated	Principal software
Lincoln-Petersen	Batch	Research	< 1 month	No	Population size		Calculator, spreadsheet, SPAS
Schnabel	Batch	Research	< 1 month	No	Population size		Calculator, spreadsheet, or CAPTURE
Removal	No mark	Research	< 1 month	No	Population size		CAPTURE or MARK
Closed-CAPTURE models	Unique individual	Research	< 1 month	No	Population size, capture probability		CAPTURE for all closed models or MARK for non-heterogeneity
Jolly-Seber and Cormack-Jolly-Seber	Unique individual	Research	>1 month	No	Population size, apparent survival	Individual growth from recaptures	POPAN, JOLLY, or MARK
Robust	Unique individual	Research	>1 month	No	Population size and growth, apparent survival, temporary emigration	Individual growth from recaptures	CAPTURE and JOLLY together or MARK
Brownie	Unique individual	Fishery	>1 year	No	Survival, total mortality		BROWNIE MARK
Hoenig/ Hearn	Unique individual	Fishery	>1 year	Yes	Survival, fishing and natural mortality		AVOCADO
Telemetry	Unique individual	Research	= 1 year	No	Survival, fishing and natural mortality	Movement, habitat use	SURVIV
Combined telemetry/ Tagging	Unique individual	Research/ Fishery	> 1 year	No	Survival, fishing and natural mortality	Movement, habitat use	SURVIV

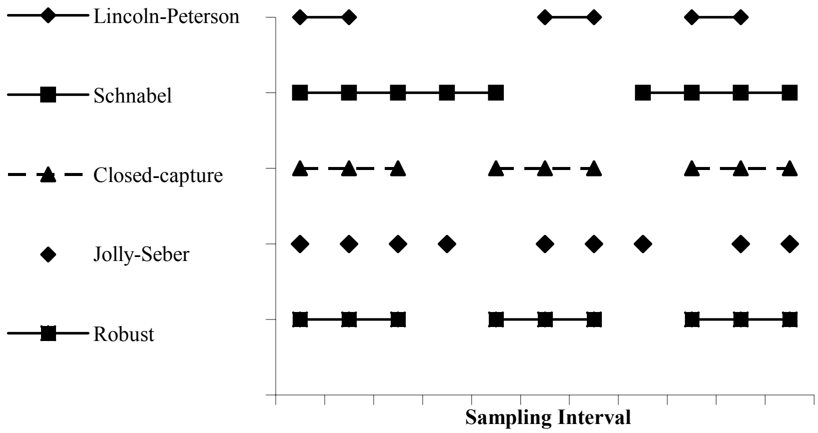

Figure 1. Diagram demonstrating assumptions about capture probabilities for each type of capture-recapture model discussed in this chapter. Each marker represents a sampling event. The solid lines connecting markers indicate closed populations with equal capture probabilities. Dashed lines between samples indicate closed populations with unequal capture probabilities. Gaps represent intervals where populations are open.

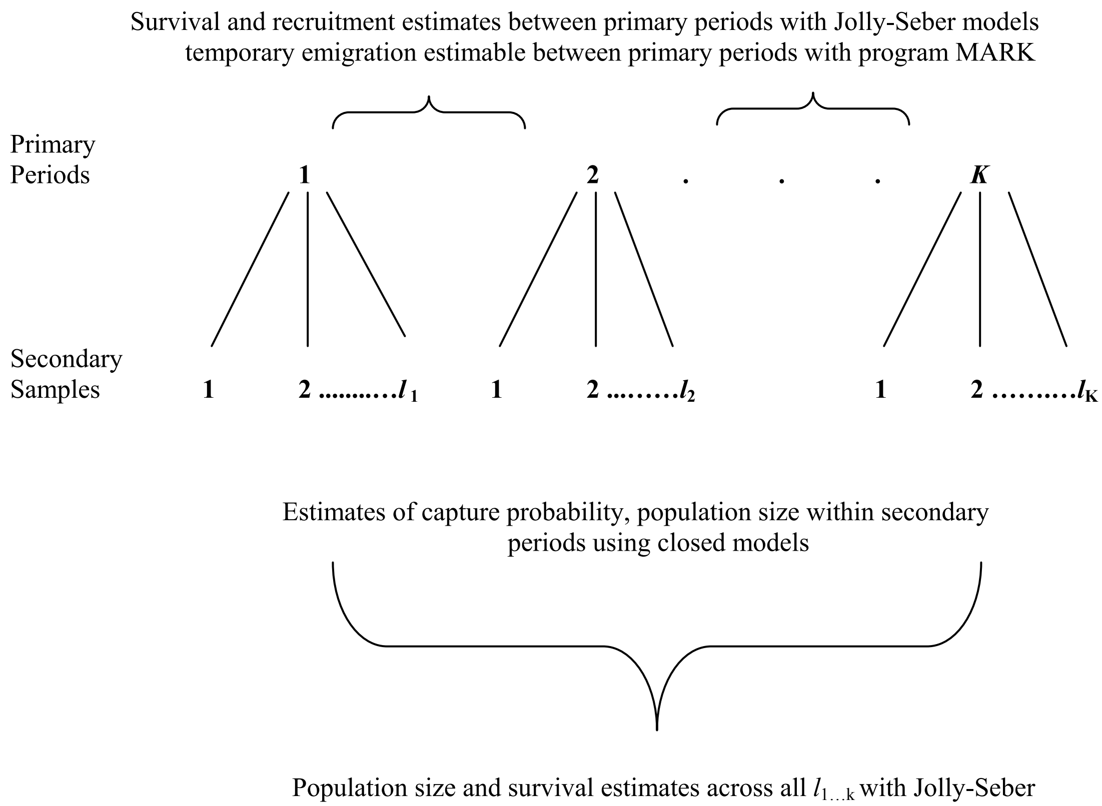

Figure 2. Schematic drawing of the robust-design model demonstrating open and closed periods as well as estimable parameters at each period.

Box 1. Planning a capture-recapture study.

A key step in planning a capture-recapture study is to examine the possible precision of parameter estimates before conducting the study. This helps determine if study objectives can be met given the expected sample sizes and variances. For example, population size estimates of an endangered species may require higher precision (as part of a recovery plan) than estimates associated with an annually stocked game fish. One simple way to do this is to use estimates or assumed values for capture probability and population size to generate expected frequencies of the possible capture histories by hand (Box 1, Table 1) or on a spreadsheet. These capture histories can then be analyzed using the software and models discussed in this review to evaluate approximate precision at different capture histories, population sizes, and number of samples.

As an example, there are eight (2^3) possible capture histories in a closed population study with three samples. Excluding the case with no captures (000), there are seven of interest to us (Box 1, Table 1). If we assume the capture probability (p) to be 0.10 based either on pilot field work or published studies, and our approximate estimate of population size (N) is 1,000 individuals, then we can calculate the expected number of fish for each capture history (Box 1, Table 1). The expected frequencies of each capture history could then be analyzed in MARK or CAPTURE to evaluate precision of parameter estimates using the various closed models discussed in this review. This very simple example does not incorporate heterogeneity. But assigning different capture probabilities to portions of the estimated population size would simulate heterogeneity.

This approach also provides insight into the amount of effort required to obtain precise parameter estimates. Precision can be improved by increasing the capture-probability (which may be difficult), increasing the number of samples, or a combination of the two. This allows biologists to examine if the potential gain in precision justifies the expense associated with increasing the sampling effort.

This approach can also be generalized in two ways. We could generate expected capture histories under a heterogeneity model and examine bias and precision of different estimators (i.e., M_t vs. M_h). We could also generate expected capture histories under an open model (i.e., Jolly-Seber) and examine precision issues under that scenario.

We encourage the use of simple pre-study evaluations such as this before conducting a capture-recapture study. Biologists should find the information from these simple simulations very useful in evaluating and planning the feasibility of a capture-recapture study. This approach should lead to savings in both time and money by implementing the most efficient study design and establishing realistic expectations for study results.

Box 1, Table 1

Approximate expected capture frequencies for a three sample closed population study with a capture probability $p = 0.1$, and estimated population size $N_t = 1{,}000$.

Capture history	**Formula to calculate expected frequency**	**Approximate expected frequency**
111	p x p x p x N	1
110	p x p x (1-p) x N	9
101	p x (1-p) x p x N	9
011	(1-p) x p x p x N	9
100	p x (1-p) x (1-p) x N	81
010	(1-p) x p x (1-p) x N	81
001	(1-p) x (1-p) x p x N	81

CHAPTER 3

ESTIMATING POPULATION SIZE OF AN INVASIVE CATFISH IN COASTAL RIVERS

Abstract

Invasive aquatic species are becoming increasingly problematic for aquatic ecologists and resource managers, as the ecological and economic impacts of introductions become better known. The flathead catfish *Pylodictis olivaris* is a large piscivorous fish native to most of the interior basin of the United States. Via legal and illegal introductions, they have been introduced into at least 13 U.S. states and one Canadian province, primarily along the Atlantic slope. I used a variety of capture-recapture models to estimate flathead catfish population parameters in three North Carolina coastal plain rivers. My estimates using a Jolly-Seber model were hindered by low capture probabilities and high temporary emigration. Reasonable estimates were calculated using a robust-design framework for population size and temporary emigration with supplemental information from a radio-telemetry study to examine model assumptions. Population size estimates ranged from 4 to 31 fish/km (>125-mm total length) of sampling reach. Additional analyses showed high rates of temporary emigration (>90%), independently supported by radio-telemetry results. This approach to population assessment, integrating the robust design with radio-telemetry, provides insights into demographics and behavior that are applicable to developing a broad understanding of flathead catfish and other invasive aquatic species.

Introduction

The introduction and establishment of exotic species in aquatic environments is a poorly understood phenomenon widely considered to threaten most aquatic ecosystems. The impact of non-native species on aquatic ecosystems is varied and unpredictable (Moyle and Light 1996). Reported impacts of exotic species introduction range from integration into the introduced area with no apparent impact to natives (Wikramanayake 1990), to widespread declines or extinctions of native species and cascading negative impacts on ecosystems and their human users (Moyle and Light 1996; Folkerts 1999; Kolar and Lodge 2000).

Knowing the abundance of an invasive species is particularly important in assessing the "success" of the invasion, the threat of spread, or options related to potential control activities. Estimating the relative abundances of native and exotic species within estuaries and monitoring these populations through time was recently identified as the second highest research priority by the U.S. National Estuarine Research Reserve System (Wasson et al. 2002). Aquatic environments present unique challenges to researchers in assessing exotic and native species abundance beyond those of terrestrial studies because of logistic and sampling difficulties imposed by aquatic habitats. These sampling difficulties further exacerbate the central problem in many capture-recapture studies of obtaining sufficient accuracy and precision in estimation methods to develop a meaningful inference of population size.

Investigations of population dynamics often employ a wide variety of parameters, including population size, population and individual growth rates, emigration, immigration, and birth/death rates. Complete censuses of a population are rarely possible (Pollock et al. 1990; Lancia et al. 1994) and determining population size of an aquatic invader is potentially more difficult due to limited knowledge of the invader's habitat use, life history, or uncertain susceptibility to standard sampling gears.

A diverse array of models and techniques has been developed to generate estimates of population demographics for animal populations using capture-recapture methods (Williams et al. 2002). Under appropriate sampling conditions, these approaches are well suited to generate accurate and precise estimates of population size and examine the population parameters (births, deaths, immigration, emigration) shaping exotic populations.

Capture-recapture models are classified by whether the populations are open to births, deaths, immigrants, emigrants, and permanent deletions (open models) or the population size is constant during the study period (closed models). These models and their application are reviewed in Chapter 2. I incorporate both approaches in this study and discuss how violations of these assumptions affect model estimates. I also utilize auxiliary information from a concurrent radio-telemetry study to evaluate how well the assumptions of the capture-recapture models were met and to enhance our understanding of this aquatic invader.

Study Species

The flathead catfish *Pylodictis olivaris* is a large piscivorous catfish native to the Rio Grande River, Mississippi River, and Mobile river drainages (Smith-Vaniz 1968; Jenkins and Burkhead 1994) and introduced into at least 13 other states, including North Carolina (Jackson 1999). The only documented introduction of flathead catfish into North Carolina waters was in 1966 by an unauthorized release of 11 adults (total weight 107 kg) into the Cape Fear River near Fayetteville (Guier et al. 1981). Within 15 years following introduction, flathead catfish had expanded to populate a 200-km section of the river and had emerged as the dominant predator within the Cape Fear River system (Guier et al. 1981). The current distribution of this species in North Carolina includes most major river drainages.

Flathead catfish demonstrate high individual and population growth rates (Guier et al. 1981; Quinn 1989; Munger et al. 1994; Nash and Irwin 1999), rapid range expansion (Guier et al. 1981; Ashley and Buff 1987; Jenkins and Burkhead 1994), and carnivorous food habits (Swingle 1967; Quinn 1989; Ashley and Buff 1987). Maximum size of flathead catfish in North Carolina (from angling records) is currently 56% by weight of the world record collected in Kansas (31.8 kg NC; 56.4 kg KS). Stomach content analysis of this species in introduced areas has shown high occurrence of native ictalurids, centrarchids, and clupeids (Guier et al. 1981; Ashley and Buff 1987) leading to widespread angler and management agency concern over declining populations of native redbreast sunfish *Lepomis auritus* (Guier et al. 1981; Ashley and Rachels 1998) in several rivers along the southeastern Atlantic slope.

Given the characteristics and observations described above, resource managers in areas where flathead catfish have been introduced are concerned with the potential impacts to native fish communities following flathead catfish introduction. Here I examine population size for introduced populations of flathead catfish and relate these demographic parameters to time elapsed since each population's introduction.

Methods

Study Sites

Three primary study rivers of similar size (mean width ~50 m each; Northeast Cape Fear River, Cape Fear River Drainage; Contentnea Creek, Neuse River Drainage; Lumber River, PeeDee River Drainage) located in the coastal plain region of eastern North Carolina were selected for study with assistance from North Carolina Wildlife Resources Commission (NCWRC) biologists. Flathead catfish presence in each of these rivers had been documented by routine sampling as part of a long-term fish community monitoring conducted by NCWRC personnel with the Northeast Cape Fear River supporting the oldest documented population (introduced for about 30 years), followed by Contentnea Creek (about 15 years) and the Lumber River (< 5 years). I sampled flathead catfish in fixed sample reaches adjacent to long-term NCWRC sampling locations. Two adjacent 1-km reaches were sampled in both Contentnea Creek and the Lumber River, and 3 adjacent 1-km reaches were sampled in the Northeast Cape Fear River. Due to debris blocking the river (2001 and 2002) and low water conditions (2002) in the Lumber River, one of the reaches was divided into two parts, thus catch per unit effort is reported from three reaches in that river.

Collection

Fish were collected using low-frequency electrofishing (Smith-Root Inc. Model GPP 7.5 pulsed-DC, 1.5-2.0 A, 15 pulses/sec), a capture technique that has been shown to be the most effective non-lethal collection technique for flathead catfish (Justus 1996; Stauffer and Koenen 1999). All flathead catfish collected were weighed (g) and measured (TL mm). Flathead catfish >115 mm but <254 mm TL were tagged with a 12-mm Passive Integrated Transponder tag (PIT) in the dorsal musculature behind the dorsal spine (as documented for channel catfish *Ictalurus punctatus*, Moore 1992). An alternative location to the dorsal musculature was employed for large (>254-mm TL) fish to reduce possibility of tag consumption by anglers. Fish > 254-mm were tagged in the head musculature posterior to the eye socket with 14-mm PIT tags. Tag insertion locations were sealed with surgical adhesive (butyl cyanoacrylate). All fish also received a circular anal fin clip as a secondary batch mark to estimate tag loss. Prior to field studies, preliminary lab experiments indicated that tag retention was high, fish behavior did not appear to be affected by tagging, and mortality (from tag implantation or increased predation risk due to tagging) did not appear to differ from non-tagged flathead catfish (W. E. Pine, *unpublished data*).

Population Models

Because sampling efforts usually do not collect every individual in a population, estimates of population size should incorporate a probability function of detecting an animal (capture probability), given that the animal is available to be captured (animal is alive and present in the sample area; Chapter 2). This capture probability is especially important in establishing the presence of an invasive species and may be used to adjust counts of fish collected to actual abundance by estimating animals that are present, yet not collected.

Although flathead catfish are widely distributed throughout the interior of the US and support important recreational and commercial fisheries throughout their range (Pitlo 1997; Travnichek and Clemmons 2001), little published information exists on their life history, behavior, or population demographics. Because of this dearth of information, particularly related to movement patterns, which should be considered in designing a capture-recapture study, I initially used Jolly-Seber open population models to estimate population size (Method 1 below). I then incorporated information from these Jolly-Seber models and auxiliary radio telemetry data into a combined open and closed population modeling framework (Method 2 below; Pollock's Robust Design, Pollock 1982; Pollock et al. 1990; Chapter Two) and compared the two approaches. Fish were collected in each reach from late spring through early fall, during the times fish were susceptible to electrofishing (generally when water temperatures exceeded 18 C, Figure 1).

Method 1: Jolly-Seber Open Models

Estimates of population size ($\hat{N}_i$), capture probability ($\hat{p}_i$), and apparent survival ($\hat{\phi}_i$) among all samples were generated for each reach on all rivers. Low recapture rates precluded estimation of some parameters on the Northeast Cape Fear River and many parameters on the Lumber River.

Population size was calculated in 2001 and 2002 for each sample reach using models developed by Cormack (1964), Jolly (1965), and Seber (1965) (Jolly-Seber models, JS) with a general form of:

$$\hat{N}_i = \frac{n_i}{\hat{p}_i} \tag{1}$$

where:

$\hat{N}_i$ = estimated population size,

n_i = number of marked and unmarked animals captured in the *i*th sample, and

$\hat{p}_i$ = estimated recapture probability for animals collected in the i^{th} sample.

The population size estimates were averaged over all of the sampling periods to generate an annual estimate of population size ($\hat{N}_{year}$). Estimates of population size, capture probabilities, and associated variances were calculated using program MARK (Burnham and Anderson 1998).

Four possible open population models were fit to data from each reach in program MARK (Table 1). These models contained two parameters, survival ($\hat{\phi}_i$) and estimated capture probability ($\hat{p}_i$), and allowed each parameter to be either constant across all sampling events (.)

or variable for each sampling event (*t*) (Table 1). Parameter estimates were constrained between zero and one.

Model selection was based on Akaike's Information Criterion (AIC_c) (Akaike 1973) adjusted to account for small sample size (Burnham and Anderson 1998). Parameters with nonsensical values (e.g., infinitely large standard errors) were used as an indicator of poor model fit to the data. I used the AIC_c value and biological information to select the most realistic model with the highest precision and least amount of bias (Burnham and Anderson 1998).

<u>Method 2: Robust Design Models</u>

Open population models assume that all animals are equally likely to be captured in each sampling period and any emigration is permanent (Pollock 1982; Pollock et al. 1990). These assumptions are often difficult to meet, and several modifications to open population models have been designed to compensate for violating the emigration assumption (Kendall et al 1999; Williams et al. 2002). I used Pollock's (1982) "robust design" to estimate population size within 5-day "secondary" sample periods, and open JS type models to estimate survival, immigration, and emigration between monthly "primary" periods (Pollock 1982; Pollock et al. 1990; Kendall et al. 1997). This sampling design requires that secondary samples are collected over short time periods where the population is assumed closed (Chapter 2).

Traditional open population models assume that all emigration from the study area is permanent. However natural movement patterns of the study animal can lead to situations where individuals are entering and leaving the study reach repeatedly, creating temporary emigration (Chapter 2). Kendall et al. (1997) described temporary emigration as either "Markovian" where an animal "remembers" that it has left the study area and returns based on some time-dependent function, or "random" where the animal leaves for one sampling event, then returns (but can emigrate randomly again). Basically the presence of a Markovian emigrant in a sample is dependent on the location of the animal in the previous sampling period (i.e., was the animal available for capture in the sampled area?), whereas the presence of a random emigrant does not depend on its location in the previous sample period. I fit models to the data collected under a robust framework that accounted for both types of emigration.

Four robust design models were fit to each reach in each river for the 2002 data (Table 1). I fit two "classic" robust design models; one model fixed apparent survival equal to 1, and the other allowed survival to vary across sampling time. The classic robust models did not allow for temporary emigration. I then fit two models incorporating temporary emigration (random, G'' and Markovian, G'). Apparent survival across primary periods was fixed at 1 for each temporary emigration model to allow model convergence. Fishing and natural mortality were likely low for this species over the short summer period evaluated in this study.

Incorporating radio-telemetry information

A concurrent study on flathead catfish habitat use and movement patterns in the same study reaches in each river (NCWRC Final Report) provided important information related to population model assumptions. Twenty-two fish were collected in Contentnea Creek, and twelve each in the Northeast Cape Fear River and Lumber River (within the sample reaches) and surgically implanted with radio transmitters. I used these radio-tagged fish as a known population to help evaluate whether emigration was occurring from my study reaches and also to empirically estimate capture probability. Capture probability was estimated by examining the number of radio-tagged fish collected in electrofishing samples vs. the number of radio-tagged fish available for capture in the sampled reach. Searches for radio-tagged fish in the sample reaches occurred immediately after processing fish collected during the electrofishing sampling. This auxiliary information was then incorporated when possible into population models described above and used to evaluate population model assumptions.

Results

Catch-per-effort

During the intensive sample period from mid-May to early-September, mean catch-per-hour was low and variable in each year at all sample reaches on each river (Table 2). Mean flathead catfish catch-per-hour ranged from 8.8-16.6 in Contentnea Creek, 3.2-6.9 in the Northeast Cape Fear River, and 0.3-15.2 in the Lumber River. In 2001 sampling was concentrated in Contentnea Creek because of low capture rates in the Northeast Cape Fear and Lumber Rivers, while in 2002 sampling was evenly distributed across rivers.

Seasonal catch rates

Catch rates varied substantially between seasons. Highest catch rates were generally observed in each river during late spring through fall when water temperatures exceeded 18 C. Because of low catch rates during cool seasons (Figure 1), sampling was conducted during late spring through early fall.

Tag loss

Approximate tag loss based on recapture rates of fin-clipped fish that lost their PIT tag show that tag loss is about 4% (2000-2002 Contentnea Creek 7 tags lost / 157 recaptures of previously PIT tagged fish). Tag loss can positively bias population size and negatively bias survival estimates and recapture probabilities. My population and survival estimates presented are not adjusted for this minimal rate of tag loss and this should be considered in evaluating results for all parameter estimates.

Jolly-Seber Results

Contentnea Creek

Reaches 1 and 2 were sampled 19 and 15 times, respectively, each in 2001. Ninety-six fish were collected once in reach one, 14 were captured twice, 5 were captured three times, 1 was captured four times, and 1 was captured five times. In reach two, 108 fish were captured once, 13 were captured twice, and 4 fish were captured three times. Unfortunately, the only model that was able to fit the data for either reach was a fixed apparent survival and capture probability model for reach 2 ($\hat{\phi}_.$, $\hat{p}_.$, Table 3, Figure 1). Other models would not fit the data because of extremely low recapture rates and violations of several of the assumptions of open population models (see discussion). Capture probability estimates for the model ($\hat{p}_i$ = 0.03, SE = 0.01, Table 3) were expectedly low given the infrequency with which I collected PIT tagged fish. Apparent survival estimates were high ($\hat{\phi}$ = 0.80, SE = 0.03, Table 3). However, it is not possible to separate mortality from emigration (true survival = 1 – mortality – emigration); thus, any emigration confounds survival estimates. Based on additional information provided by my subset of radio-tagged fish, emigration (permanent and temporary) was occurring from sample reaches.

Population size estimates were generated using equation 1. The mean population size for the $\hat{\phi}_.$, $\hat{p}_.$ model (mean = 333, SE = 54, Table 3) fluctuated greatly throughout the sampling period (Figure 2). I evaluated model sensitivity to moderate changes in apparent survival and found that parameter estimates using these models did not change between $\hat{\phi}$ = 0.85 to 1.0.

My empirical estimate of capture probability for 2001 was similar to the estimate from the $\hat{\phi}_{.}$, $\hat{p}_{.}$ model. There were 82 possible collections of radio-tagged fish in the sample reaches (reaches 1 and 2 combined) during 2001. Only four radio-tagged fish were captured resulting in a capture probability estimate of 0.05. Two models with this capture probability were then fit to the data from reach 1 and 2 using MARK ($\hat{\phi}_t$, $\hat{p}_{=0.05}$ and $\hat{\phi}_{.}$, $\hat{p}_{=0.05}$). Only the $\hat{\phi}_{.}$, $\hat{p}_{=0.05}$ model from reach 2 adequately fit the data (Table 3). Survival estimates were higher for this model ($\hat{\phi}$ = 0.99, SE = 0.004) than for the $\hat{\phi}_{.}$, $\hat{p}_{.}$ model ($\hat{\phi}_{.}$ = 0.80, SE = 0.03, Table 3). Again, this estimate is likely confounded by temporary emigration. Population size estimates were lower for this model with mean population size = 200 (SE = 32).

Each reach was sampled 12 times during 2002, and I attempted to fit these data with Jolly-Seber models. Forty-six fish were collected once and 12 fish were collected twice in reach 1. In reach 2, fifty-one fish were collected once, 5 fish twice, and 2 were collected three times. For comparative purposes, the same four open models were fit for both reaches during year two. The only open population model that adequately fit the data was a $\hat{\phi}_{.}$, $\hat{p}_{.}$ (constant survival and capture probability) for reach 1 in 2002. No open population model adequately fit the data for reach 2 in 2002 (parameter estimates were nonsensical). Capture probability estimates for reach 1 were expectedly low ($\hat{p}$ = 0.10, SE=0.02, Table 3). Survival estimates were high for reach 1 (reach 1 $\hat{\phi}_{.}$ =0.95, SE = 0.02, Table 3). Population size estimates were made for the 12 samples using equation 1 (mean = 116, SE = 17, Table 3).

In 2002, 4 out of 57 possible captures of radio-tagged fish were made. Open population models were fit to the data for reach 2 using the empirical capture probability estimate (empirical

$\hat{p}$ = 0.07) . I was only able to fit a $\hat{\phi}_{.}$, $\hat{p}_{=0.07}$ model to the data. Survival estimates using the empirical capture probability were higher than the $\hat{\phi}_{.}$, $\hat{p}_{.}$ model ($\hat{\phi}_{.}$ = 0.98, SE = 0.01). Mean population size was similar for this reach (mean = 138, SE = 38, Table 3) as for reach 1 using a $\hat{\phi}_{.}$, $\hat{p}_{.}$ model.

Northeast Cape Fear River

Because of low catch rates in each reach, I combined the three contiguous 1-km reaches into a single reach. Low recaptures precluded parameter estimation using all models in 2001. In 2002, 47 fish were collected once and five fish collected twice. The $\hat{\phi}_{.}$, $\hat{p}_{.}$ model was the only open model that fit data collected in 2002 (Table 3). Survival estimates using this model were extremely low ($\hat{\phi}$ = 0.02, SE = 0.04, Table 3), likely due to high emigration rates (Table 5). Capture probability was also low ($\hat{p}$ = 0.04, SE = 0.02, Table 3). Estimated population size for each km of the reach averaged 9 fish (SE = 2). As in Contentnea Creek, the radio-tagged flathead catfish demonstrated temporary emigration occurring within the sample reach in Northeast Cape Fear River with most radio-tagged fish leaving the sampling area for varying time periods only to return to the sample area.

In 2002, there were 70 possible collections of radio-tagged fish in the Northeast Cape Fear River. Only 3 of these fish were collected resulting in an empirical $\hat{p}$ of 0.04, the same as the model estimated $\hat{p}$. I fixed capture probability to the empirical estimate and re-fit the data to the same open models as described above. Again, only the $\hat{\phi}_{.}$, $\hat{p}_{0.04}$ model fit, and parameter estimates were the same as those from the $\hat{\phi}_{.}$, $\hat{p}_{.}$ model ($\hat{\phi}$ = 0.02, SE = 0.04; $\hat{N}$ = 9, SE =2, Table 3).

Lumber River

Due to low catch and recapture rates, likely due to low water levels resulting from record drought (USGS Water Resources of North Carolina), estimating population size for the Lumber River flathead catfish population was not possible. During 2002, only 19 fish were collected once and two fish were collected twice. Thus, a minimum population size for those reaches is 11 fish/km based on the number of fish collected divided by the river length sampled.

Meeting open-model assumptions

Because of additional insight into flathead catfish behavior provided by the subset of radio-tagged fish, it is unlikely that any of the estimates from the open population models are accurate. Open population models assume that any emigration is permanent. Analysis of the radio-tagged fish movement patterns revealed flathead catfish were exhibiting temporary emigration from the study reach in both Contentnea Creek and the Northeast Cape Fear River. The implications of this emigration are examined in the discussion.

Robust Design Results

Contentnea Creek

2002 sampling data were collected under a robust design with month as the primary period (four months; May, June, July, and August), and three, one-day samples within a one-week period as the closed secondary samples each month. The best-fit model for reach 1 was the random temporary emigration model (Table 4). Temporary emigration was very high (temporary emigration, G'' = 0.94, SE = 0.03, Table 5). Capture probability estimated with this model was higher than with the Jolly-Seber open population model (robust design temporary emigration model $\hat{p}$ = 0.36, SE 0.11, Table 5). Robust design models also estimate recapture probability (probability of being recaptured in the secondary sampling period). Recapture probability ($\hat{c}$) was 0.11 (SE = 0.04, Tables 4, 5). Population size estimated for each primary period was lower for the robust models than the Jolly-Seber open population models (N range 14-26 fish/km, Table 5, Figure 4). The classic robust design model fit nearly as well as the random temporary emigration model (Table 4). The survival estimate under this model was low ($\hat{\phi}$ = 0.15, SE = 0.07), likely because it was confounded with emigration (which was high). Population size estimates were similar between the random temporary emigration model and the classic robust model ($\hat{N}$ range 16-30 fish/km, Table 5).

The information from the radio-tagged fish was then incorporated by fitting three additional random temporary emigration models fixing $\hat{p}_{0.07}$, $\hat{c}_{0.07}$, and both $\hat{p}$ and $\hat{c}$ = 0.07 while keeping $\hat{\phi}$ = 1 and allowing population size to change through time. These three models were then compared to the best random temporary emigration described above which did not incorporate information from the telemetered fish (Table 6). The best fit model was the random temporary emigration model with capture probability from the radio tags ($\hat{c}_{0.07}$) while the second best model was the original random temporary emigration model without temporary emigration (Table 6). Initial capture probabilities ($\hat{p}$) were the same between these two models as were other parameter estimates (G'' = 0.94, SE = 0.03; $\hat{p}$ = 0.36, SE 0.11; $\hat{N}$ range 14-26 fish/km, Table 7). Using only the empirical capture probabilities from the radio-tagged fish ($\hat{p}_{0.07}$, $\hat{c}_{0.07}$) resulted in larger population size estimates ($\hat{N}$ range 20–143 fish/ km) than the other models ($\hat{N}$ range 14-26 fish/km, Table 7).

In reach 2, the random temporary emigration model was again the best model with high random emigration (temporary emigration, G'' = 0.93, SE = 0.02, Table 5). Estimated capture probability was higher in reach 2 than in reach 1 ($\hat{p}$ = 0.53, SE 0.08, Table 5) but recapture probability was lower ($\hat{c}$ = 0.01 SE = 0.01, Table 5). Population size estimates in reach 2 were similar in size ($\hat{N}$ range 14-31 fish/km, Table 5) to reach 1 (Table 5, Figure 3).

The same three additional random temporary emigration models using information from the radio-tag fish were also fit to the data from reach 2 as in reach 1. In reach 2, the best fitting model did not include any fixed parameters based on information from the radio-tagged fish (Table 6). The second best fitting model was the random temporary emigration model with fixed capture probability from the radio tags ($\hat{c}_{0.07}$). Again, parameter estimates were similar between the models (G'' = 0.93, SE = 0.02; $\hat{p}$ = 0.53, SE 0.08; $\hat{N}$ range 14-31 fish/km, Table 7). The model with the highest AIC_c, value used only the empirical capture probabilities from the radio-tagged fish ($\hat{p}_{0.07}$, $\hat{c}_{0.07}$) and population size estimates were larger ($\hat{N}$ range 20–143 fish/ km) than population estimates from the other models ($\hat{N}$ range 14-31 fish/km, Table 7).

Northeast Cape Fear River

In 2002, sampling in the Northeast Cape Fear River was conducted in a similar robust design framework as in Contentnea Creek. The best-fit model was a classic robust design model with fixed survival (Table 4). The survival estimate from this model was extremely low ($\hat{\phi}$ = 0.05, SE = 0.04, Table 5), likely because of high emigration from the study reach. Capture probability was much higher ($\hat{p}$ = 0.41, SE = 0.11, Table 5) than recapture probability ($\hat{c}$ = 0.05, SE = 0.03, Table 5). The population size range for the reach ($\hat{N}$ range 4-9 fish/km) for the robust design model was similar to the mean for the open model (open model mean $\hat{N}$ = 9, SE = 4, Tables 3, 5, Figure 4).

The random temporary emigration model also fit fairly well (Table 4), but gave very different estimates. Temporary emigration was high (G'' = 0.97, SE = 0.02, Table 5). Capture and recapture probabilities were similar to the classic robust design model ($\hat{p}$ = 0.41, SE = 0.11; $\hat{c}$ = 0.05, SE = 0.03, Table 5). Population size estimates were similar to the classic robust model ($\hat{N}$ range 4-9 fish/km, Table 5, Figure 4). Although the classic robust design estimate with fixed survival had the lowest AIC_c value, the random temporary emigration model is likely a more biologically meaningful model because temporary emigration was occuring and can be accounted for in the model.

As in Contentnea Creek, information from the radio-tagged fish was incorporated into additional random temporary emigration models. In the Northeast Cape Fear River, the best fitting model included a fixed $\hat{c}$ based on recaptures of the radio-tagged fish ($\hat{c}_{0.04}$) (Table 6). This is similar to the results for reach 1 in Contentnea Creek. The second best fitting model was the same random temporary emigration model as above which did not include any fixed parameters from the radio-tagged fish. Population parameter estimates were again similar between the models (G'' = 0.97, SE = 0.02; $\hat{p}$ = 0.41, SE 0.11; $\hat{N}$ range 4-9 fish/km, Table 7). Population estimates using only the empirical capture probabilities from the radio-tagged fish ($\hat{p}_{0.04}$, $\hat{c}_{0.04}$) were larger ($\hat{N}$ range 26–61 fish/km) than population estimates from the other models ($\hat{N}$ range 4-9 fish/km, Table 7).

Discussion

Population size estimation

Low recapture rates observed in all rivers prevented most population models from fitting the data. These low recapture rates are possibly a function of the flathead catfish population frequently "turning over" with the majority of the tagged fish moving out of the sampling area and a new sub-population of fish moving in regularly. The cue for this turnover is not apparent, but possible factors include changes in water level or prey availability. Strong annual movement patterns appear to be related to spawning migration (NCWRC Final Report). Low catch rates are also likely a function of poor efficiency of electrofishing gear for collecting flathead catfish in these waters.

Temporary emigration is known to bias estimates of many population parameters (N, ϕ, p) (Pollock et al. 1990; Kendall et al. 1995; Kendall et al. 1997; Zehfuss et al. 1999). I quantified temporary emigration under a completely random framework using the robust design. The estimates of G'' from each reach and river indicated that most tagged fish (~90%) emigrated from the sample reach and were thus unavailable for capture at the following sample event. The number of these PIT tagged fish that are "temporary" emigrants and later return to the sampling reach during the sampling time is not known. Further examination of the radio-tagged fish provides insight as to which fish are permanent emigrants and which are temporary emigrants. The majority of radio-tagged fish in this study in each river demonstrated strong seasonal movement patterns from the tributary to mainstem rivers beginning in late spring and progressing through summer (NCWRC Final Report). Flathead catfish then returned to the tributaries in the spring, only to repeat the same movement process. However, the radio-tagged fish revealed temporary emigration in all rivers within the summer. In each river, individual radio-tagged fish left for several days or weeks, and then returned to the sample reach. The radio-tagged fish provided valuable information with which to evaluate sample design and population model assumptions in addition to the migration and life history information provided (NCWRC Final Report).

Burnham (1993) demonstrated that under a completely random emigration model, traditional Jolly-Seber survival estimates are relatively unbiased by emigration, although their precision is reduced. My survival estimates under the best Jolly-Seber models in Contentnea Creek were high (>80%) and corresponding standard errors low (Table 3). I expected survival to be high given low rates of angling or natural mortality, as well as the short time period (about 4 months) over which this analysis was conducted. Although standard errors were low over the time period I evaluated, over a longer time period the precision may be reduced as in Burnham (1993).

Kendall et al. (1997) and Kendall (1999) demonstrated that when the primary research interest is in the "superpopulation" inhabiting the general area around the study reach that parameters of interest (p , ϕ , N) are not biased by temporary emigration. Thus, under the completely random emigration model, my parameter estimates within the specific primary reach or secondary may apply to a more general area of Contentnea Creek. It is difficult to define the geographic bounds of a superpopulation in a riverine setting. Although it is not likely that the superpopulation in this case would characterize flathead catfish population size for the entire Neuse River basin, it may represent a short-term carrying capacity for an area of river that offers "desirable" habitat (e.g., based on spawning sites early in the spring or optimal deep water structure later in the summer) at that time. For example, the general area of Contentnea Creek between the upstream boundary of my sampling reach and the creek mouth (approximately 7-km) contains about 3 km of "optimal" habitat, two of which include my sample reaches (NCWRC Final Report). My estimates of population size and survival may apply then to a superpopulation (the population of fish in the 3-km section of preferred habitat) in this area of Contentnea Creek. The relationship between population size estimates collected from defined areas (e.g., 1-km sampling reach) and an area with very large boundaries (e.g., Neuse River system), which may contain a superpopulation, should be explored further.

One option to increase capture probability would be to increase the size of the area sampled. However, additional analysis using combined data from the two sample reaches in Contentnea Creek did not result in an increase in capture probability. This is likely because flathead catfish moved a greater distance than the combined 2-km sample reach. However, increasing the sampling area by combining the three continuous reaches in the Northeast Cape Fear River allowed estimates to be generated, whereas individual 1-km reaches estimates were not possible.

For some fish populations, increasing sampling effort (time expended electrofishing) may increase capture probability, but this is not the case with flathead catfish. On several occasions I attempted to collect additional flathead catfish known to be present in the area (radio-tagged fish) using multiple electrofishing passes through the sample reach. Using this approach I rarely collected the known fish, or any additional flathead catfish. Mesa and Schreck (1989) demonstrated that trout behavior was altered for at least 24-h following electrofishing and marking. A similar response in flathead catfish could explain why it was difficult to capture flathead catfish with additional sampling in the area.

Incorporating radio-telemetry information

I used the observed capture rates of the radio-tagged fish as empirical estimates of capture probability and recapture probability and these estimates were similar to the $\hat{p}$ estimates from the Jolly-Seber models (Table 3). However, the radio-tag based estimates are not similar to any of the $\hat{p}$ estimates from the best robust design models (Table 5). Surprisingly, in each of temporary emigration robust design models, the estimated $\hat{p}$ from the radio tags is actually much closer to the $\hat{c}$ (recapture probability) (Table 5). In the Northeast Cape Fear River and in reach 1 in Contentnea Creek, the additional robust design models incorporating telemetry information were selected as the best model only if the radio-tag capture rate was used as a $\hat{c}$ (Table 6). Using the radio-tag capture rate as either $\hat{p}$ or $\hat{p}$ and $\hat{c}$ resulted in higher AIC_c values (poorer model fit) than not using the radio-tag information, or using the radio-tag information only as a $\hat{c}$ (Table 6). This indicates a lack of statistical support for using the empirical capture rates from the radio tags to fit population models.

The higher capture than recapture probabilities could demonstrate a "behavioral response" where the capture probability changes as a result of being collected previously (Williams 2002). Several closed population models exist that can account for a behavioral response (Chapter 2); however, the data collected in each of the primary periods here were too sparse to fit those models. The learning ability of fish has recently been given new attention and is likely much greater than was formerly thought (Laland et al. 2003). It may be possible that following initial capture, flathead catfish learn to avoid collection in subsequent sampling events. Mesa and Schreck (1989) documented that trout behavior was altered for 24 h following electrofishing collection and tagging and a similar behavioral response could persist longer than

24-hours in flathead catfish. If so, my samples within the primary sampling periods (collected 48-hours apart) could be affected. The learning ability or behavioral response to sampling by flathead catfish following electrofishing and tagging to avoid collection requires additional research before conclusions can be drawn.

Population estimates between the model fitted $\hat{c}$, or the $\hat{c}$ from the radio-tags do not differ because initial capture probability determines the estimates of *N* in a robust design model (Williams et al. 2001). However, the differences between using the model fit estimates of $\hat{p}$ and the $\hat{p}$ from the radio-tags is large (Table 7). This is because in each case the $\hat{p}$ estimates from the radio-tags are much lower than the model fit estimates (Table 7). Given the low statistical support for using the radio-tag $\hat{p}$ (Table 6) and the closer agreement between the model fit $\hat{c}$ with the capture probability of the radio-tagged fish, the best population estimates are likely the estimates which do not include capture or recapture probability information from the radio-tagged fish (Tables 5, 8). However, other than a behavioral response to electrofishing and radio-tag implementation, I am unable to speculate why $\hat{p}$ estimates differ between the PIT-tagged fish and the radio-tagged fish.

Comparisons to other populations

Quinn (1988) reported limited movement in an introduced flathead catfish population in Georgia. Dames et al. (1989) and Skains and Jackson (1993) both suggest that flathead catfish populations generally exhibit restricted movements and that relatively small river sections (2-km, Skains and Jackson 1993) could be treated as unique management units. These reports are similar to many fish movement studies based on tag returns or radio telemetry in that little attention is directed to the proportion of the tagged population not recaptured (Gowan et al.

1994). In studies with passive tags Quinn (1988), Dames et al. (1989), and Skains and Jackson (1993), found flathead catfish recapture rates were low (not reported, but approximately 10%, 8%, and 5%, respectively based on the number of fish recaptured / number of fish tagged in each study) and similar to the recapture rates in this study. These authors drew their conclusions of limited movement based on locations of recaptured fish. For example, Quinn (1988) reported that, "…79% of recaptured flathead catfish showed no detectable movements…" but this percentage is based on only 159 recaptures of 1,636 tagged fish. Gowan et al. (1994) review movement studies in salmonids and other fish species and suggested that, "The large number of fish never recaptured [in the study reach] certainly leaves open the possibility that many fish moved beyond the boundaries." In each of the flathead catfish studies mentioned above, the large number of tagged fish that were never recaptured are not accounted for, possibly because these fish had left the study area and thus were not available to be captured, similar to my results. Skains and Jackson (1993) simultaneously used radio-tagged flathead catfish in conjunction with their traditional passive tags in their study. These authors tagged 20 fish with radio tags, 3 of which were immediately "lost" and were assumed to have malfunctioned, been caught and removed, or move outside the study area. These authors searched outside of their study reaches (ca. 30 km) for these tagged fish and did not locate them. However, given the movement patterns I observed and other large-scale movements of flathead catfish (including tag returns >300 km from original tagging location in 76 days, Dames et al. 1989), it is possible that several of the "missing" fish in Skains and Jackson (1993) migrated large distances outside of the search area.

Few published estimates of flathead catfish population size or density, for native or introduced populations, exist for rivers or lakes to compare with my estimates. The flathead catfish population sizes in the rivers I examined are within the range of published estimates for both native and introduced populations. For native populations, Dettmers et al. (2001) report flathead catfish densities of 0.31 and 0.53 fish/ha in Pool 26 of the Mississippi River and lower Illinois River, respectively, from trawl samples. Orth (1980) reported flathead catfish density of between 3-64 fish/ha (mean = 27) from Lake Carl Blackwell, Oklahoma, collected from cove rotenone samples. In introduced populations in the Flint River, Georgia, Quinn (1988) reported flathead catfish densities of 13 fish/ha (153 fish/river km) estimated using a Schnabel estimate and 14 fish/ha (161 fish/km) using a Schumacher-Eschmeyer estimate. Quinn's estimates are much higher than abundances reported for native populations in the Missouri River (9-17 fish/km) using similar methods (Morris et al. 1971 as in Quinn (1988)). Dobbins et al. 1999 estimated the size of an introduced flathead catfish population in the Apalachicola River, Florida, to range from 35-58 fish/km of fish ≥ 380-mm TL. Population density estimates in my study ranged from 1-8 fish/ha (4-31 fish/km) > 125-mm TL (Table 8).

It is likely that in several of the studies above, some of the assumptions for the capture-recapture methods used were violated in estimating population size, biasing population estimates. Several of these studies in both native (Morris et al. 1971) and introduced populations (Quinn 1988) used closed population estimates, which are sensitive to assumption violations. The Schnabel and Schumacher-Eschmeyer are both closed population models that assume the population is "closed" to births, deaths, immigration or emigration during the study period (Chapter 2). The Quinn (1988) study took place over a six-month period from late May through

November. It is possible that during this period some changes in the population size occurred from the demographic factors listed above (e.g., births or deaths). Immigration and emigration may be less of a problem in Quinn's (1988) study than here, given the large (50-km) study area they used. Dobbins et al. also used a Schnabel estimator to estimate population size, and likely met many of the assumptions of the Schnabel model by sampling relatively large areas (8.1-km sample reaches) intensively (4-6 samples per reach) over a fairly short period (each sample separated by 5-16 days). Dobbins et al. (1999) also carefully evaluated movement patterns of flathead catfish within their sample sites by sampling in "buffer" zones that separated each sample reach to check for flathead catfish movement out of each reach. The affect that violating these assumptions would have on the population estimate would depend on which and how each assumption is violated (Williams et al. 2002) but the most likely violations of mortality or emigration from the study site would lead to positive biases in population size. However, even with the potential biases in each of the above population estimates, I suspect that North Carolina coastal rivers support flathead catfish populations that are smaller in size than introduced populations in Georgia and Florida (Table 8).

Estimated emigration rates and observed movement patterns clearly demonstrate that my sample reaches within tributaries are not discrete flathead catfish populations unique to each tributary (NCWRC Final Report). I conclude that the tributary "populations" of flathead catfish are actually extensions of populations found within each mainstem river. The information on flathead catfish movement patterns in native and introduced populations is conflicting (some suggest large movements (Dames et al. 1989), others do not (Dobbins et al. 1999 for an introduced population). Based in part on my work, I clearly showed that flathead catfish in coastal North Carolina rivers move extensively (NCWRC Final Report). These large movement patterns are presumably conducive to rapid dispersal and invasion success.

Implications for presence/absence monitoring

Electrofishing appears to be a poor early indicator of flathead catfish presence or absence. Bayley and Austen (2002) empirically estimated capture probability in ponds for a variety of fish species using an AC boat-mounted electrofisher. For their group of several catfish species, they estimated catchability to be 0.18%. My empirical capture probability (from the radio tags) and estimated capture probability from the PIT-tagged fish was much higher for flathead catfish, likely because I used direct current, lower output voltages, and pulse-rate frequency than those of Bayley and Austen (2002). The "low-frequency" DC electrofishing technique that I used is similar to that described by Quinn (1986) and is thought to be a more effective electrofishing technique for collecting catfish species (Justus 1996) than the less applicable AC electrofishing settings used by Bayley and Austen (2002).

Recommendations and conclusions

My experiences studying flathead catfish are likely similar to the difficulties encountered in studying other invasive fish species. The low capture probability for flathead catfish demonstrates the difficulty in detecting invasive species as a component of routine monitoring efforts. This could result in flathead catfish not being detected in introduced areas until populations are well established and expanding in both numbers and area occupied. By combining the capture-recapture information from my study and telemetry information from the larger NCWRC project, I was able to quickly learn detailed information on detection probability, population size, movement patterns, and habitat use– critical information required to evaluate the level of establishment and risk of spread of an aquatic invasive species. Further, my findings on migration and capture probability begin to resolve seemingly conflicting results from other flathead catfish populations. I recommend the use of a combined capture-recapture and radio telemetry study in assessing other aquatic invasive animal populations.

The ecological impact of flathead catfish in coastal North Carolina rivers is difficult to discern because of other confounding anthropogenic impacts on these river systems including introduction of other exotic species, poor water quality, and habitat degradation. Flathead catfish are well established in most major coastal North Carolina river systems and may be present at lower densities in others as well. I had originally hoped to evaluate population size estimates in relation to time of introduction at each of my study reaches. However, there appears to be no clear relationship between the age of flathead catfish introduction and my estimates of population size. While in general, Contentnea Creek appears to support slightly higher populations than the other two rivers, the high variance of most models precludes a precise statistical comparison.

Management efforts for flathead catfish should be focused on preventing the spread of this species within North Carolina and elsewhere through outreach programs designed to heighten public awareness of the threats imposed by invasive species on native fish communities. In areas where flathead catfish have become established (such as the rivers in this study), efforts should be made to encourage recreational and commercial harvest of this species (Chapter 5). Given the popularity of flathead catfish as a food fish in its native and introduced range (Jackson 1999), the large recreational and commercial fisheries interest in North Carolina (National Marine Fisheries Service 2001), the seemingly insatiable global demand for fish products, and the ability of humans to impact aquatic ecosystems through intensive fishing efforts, introduced flathead catfish may be an ideal candidate species for developing a new harvest oriented fishery.

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Table 1. Name and description of each model fit to capture-recapture data collected in each river during either 2001, 2002, or both.

Model	Description
Open Models	
MARK $\Phi_{(t)}$, $p_{(t)}$	Survival and capture probability variable, parameters constrained from 0 to 1
MARK $\Phi_{(t)}$, $p_{(.)}$	Survival varies with time, capture probability fixed, parameters constrained from 0 to 1
MARK $\Phi_{(.)}$, $p_{(t)}$	Survival fixed, capture probability varies with time, parameters constrained from 0 to 1
MARK $\Phi_{(.)}$, $p_{(.)}$	Survival and capture probability fixed, parameters constrained from 0 to 1
Robust Design Models	
$\Phi=1$, $p_{(..)}$, $\hat{c}_{(..)}$, N_t, E=0, I=0 Classic robust design	Survival=1, fixed capture and recapture probability, population size varies for each primary period, no emigration or immigration, parameters constrained from 0 to 1
$\Phi_{(..)}$, $p_{(..)}$, $\hat{c}_{(..)}$, N_t, E=0, I=0 Classic robust design	Survival, capture and recapture probability fixed, population size varies for each primary period, no emigration or immigration, parameters constrained from 0 to 1
$\Phi = 1$, $p_{(..)}$, $\hat{c}_{(..)}$, N_t, $E._t$, I. Robust design with Markovian temporary emigration	Survival=1, capture and recapture probability fixed, population size varies for each primary period, Markovian temporary emigration, parameters constrained from 0 to 1
$\Phi=1$, $p_{(..)}$, $\hat{c}_{(..)}$, N_t, E. = I. Robust design with random temporary emigration	Survival=1, capture and recapture probability fixed, population size varies for each primary period, random temporary emigration, parameters constrained from 0 to 1

Table 2. Year, river, sample reach, number of sampling days, mean catch-per-unit-effort (CPUE, fish/hour), and standard error (SE) of flathead catfish catch for each river during 2001 and 2002. All samples were collected using low-frequency electrofishing described in text. Low water in the Lumber River in 2002 prevented sampling in reach 3.

Year	**River**	**Reach**	**Number of sampling days**	**Mean CPUE (SE)**
2001	Contentnea	1	18	9.04 (4.49)
2001	Contentnea	2	18	16.62 (8.23)
2002	Contentnea	1	12	8.77 (2.53)
2002	Contentnea	2	12	11.15 (2.35)
2001	Northeast Cape Fear	1	10	5.11 (1.27)
2001	Northeast Cape Fear	2	10	6.93 (2.01)
2001	Northeast Cape Fear	3	10	5.33 (1.82)
2002	Northeast Cape Fear	1	12	3.95 (0.82)
2002	Northeast Cape Fear	2	12	4.70 (1.73)
2002	Northeast Cape Fear	3	12	3.23 (0.80)
2001	Lumber	1	8	3.52 (1.30)
2001	Lumber	2	9	3.66 (1.22)
2001	Lumber	3	6	9.46 (1.79)
2002	Lumber	1	12	2.25 (1.01)
2002	Lumber	2	12	0.32 (0.22)
2002	Lumber	3	1	15.25 (0.00)

Table 3. Open population model results for each year, river, and reach where an open model was able to fit the data. Estimated capture probability ($\hat{p}$), survival ($\hat{\phi}$), and mean population size per kilometer over the summer sampling period and associated standard errors are shown. Population estimates are biased by temporary emigration (see text).

Year	River	Reach	Open Population Model	$\hat{p}$ (SE)	Survival (SE)	Summer period mean N/km (SE)
2001	Contentnea	2	$\hat{\phi}_{.}$, p. Fixed survival, capture probability	0.03 (0.01)	0.80 (0.03)	333 (54)
2001	Contentnea	2	$\hat{\phi}_{.}$, $p_{0.05}$ Fixed survival, empirical capture probability	0.05 based on radios	0.99 (0.004)	200 (32)
2002	Contentnea	1	$\hat{\phi}_{.}$, p. Fixed survival, capture probability	0.10 (0.02)	0.95 (0.02)	116 (17)
2002	Contentnea	2	$\hat{\phi}_{.}$, $p_{0.07}$ Fixed survival, empirical capture probability	0.05 based on radios	0.99 (0.01)	138 (38)
2002	NECFR	All	$\hat{\phi}_{.}$, p. Fixed survival, capture probability	0.04 (0.02)	0.02 (0.04)	9 (2)

Table 4. River, reach, model name, AIC_c value, delta AIC_c, AIC_c weight, and number of model parameters for each robust design model fit to the data. Bold indicates best-fit model with lowest AIC_c value and highest AIC_c weight.

River	Reach	Robust Design Model	AIC_c	Delta AIC_c	AIC_c Weight	Number of parameters
Contentnea	1	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E=0, I=0 Classic robust design	13.43	4.98	0.05	6
Contentnea	1	$\hat{\phi}_{.}$, p.., $\hat{c}$.., N_t, E=0, I=0 Classic robust design	10.18	1.73	0.24	7
Contentnea	1	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, $E._t$, I. Markovian temporary emigration	11.21	2.75	0.14	9
Contentnea	1	**$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.** **Random temporary emigration**	**8.45**	**0.00**	**0.57**	**7**
Contentnea	2	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E = 0, I = 0 Classic robust design	-32.46	20.22	0.00	6
Contentnea	2	$\hat{\phi}_{.}$, p.., $\hat{c}$.., N_t, E = 0, I = 0 Classic robust design	-30.13	22.55	0.00	7
Contentnea	2	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, $E._t$, I. Markovian temporary emigration	-51.76	0.92	0.39	8
Contentnea	2	**$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.** **Random temporary emigration**	**-52.7**	**0.00**	**0.61**	**6**
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E=0, I=0 Classic robust design	-2.85	9.55	0.01	6
NECFR	ALL	**$\hat{\phi}_{.}$, p.., $\hat{c}$.., N_t, E=0, I=0** **Classic robust design**	**-12.40**	**0.00**	**0.78**	**7**
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, $E._t$, I. Markovian temporary emigration	-6.87	5.53	0.05	9
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I. Random temporary emigration	-9.27	3.13	0.16	7

Table 5. River name, sample reach, model name survival rate ($\Phi \pm$ SE), emigration rate ($G'' \pm$ SE) between primary periods 1 and 2, emigration rate ($G'' \pm$ SE) between primary periods 2 and 3, immigration rate ($G' \pm$ SE), capture probability ($\hat{p} \pm$ SE), recapture probability ($\hat{c} \pm$ SE), and population size per-km ($N \pm$ SE) for each primary period in 2002 using the robust design models described in text. Estimates from the Northeast Cape Fear River are converted to 1-km for comparison to Contentnea Creek. Bold indicates best fit model (lowest AICc). Blanks indicate parameters that were not components of some models simulated. "NE" are non-estimable model parameters or standard errors that result from poor model fit due to sparse data.

River	Reach	Robust Design Model	Survival (SE)	G'' (SE) Periods 1-2	G'' (SE) Periods 2-3	G' (SE)	$\hat{p}$ (SE)	$\hat{c}$ (SE)
Contentnea	1	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E=0, I=0 Classic robust design	1.00 (0.00)	0.00 (0.00)		0.00 (0.0)	0.02 (0.01)	0.11 (0.04)
Contentnea	1	Φ., p.., $\hat{c}$.., N_t, E=0, I=0 Classic robust design	0.15 (0.07)	0.00 (0.00)		0.00 (0.0)	0.30 (0.12)	0.11 (0.04)
Contentnea	1	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, $E_{\cdot t}$, I. Markovian temporary emigration	1.00 (0.00)	1.00 (NE)	0.89 (0.07)	0.97 (0.03)	0.36 (0.11)	0.11 (0.04)
Contentnea	**1**	**$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.** **Random temporary emigration**	**1.00 (0.00)**	**0.94 (0.03)**	**0.94 (0.03)**	**0.94 (0.03)**	**0.36 (0.11)**	**0.11 (0.04)**
Contentnea	2	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E = 0, I = 0 Classic robust design	1.00 (0.00)	0.00 (0.00)		0.00 (0.0)	0.02 (0.01)	0.01 (0.01)
Contentnea	2	$\hat{\phi}_.$, p.., $\hat{c}$.., N_t, E = 0, I = 0 Classic robust design	0.81 (0.42)	0.00 (0.00)		0.00 (0.0)	0.04 (0.04)	0.01 (0.01)
Contentnea	2	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, $E_{\cdot t}$, I. Markovian temporary emigration	1.00 (0.00)	NE (NE)	0.90 (0.05)	0.91 (0.04)	0.53 (0.08)	0.01 (0.01)
Contentnea	**2**	**$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.** **Random temporary emigration**	**1.00 (0.00)**	**0.93 (0.02)**		**0.93 (0.02)**	**0.53 (0.08)**	**0.01 (0.01)**
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E=0, I=0 Classic robust design	1.00 (0.00)	0.00 (0.00)		0.00 (0.00)	0.01 (0.01)	0.05 (0.03)
NECFR	**ALL**	**$\hat{\phi}_.$, p.., $\hat{c}$.., N_t, E=0, I=0** **Classic robust design**	**0.05 (0.04)**	**0.00 (0.00)**		**0.00 (0.00)**	**0.41 (0.11)**	**0.05 (0.03)**
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, $E_{\cdot t}$, I. Markovian temporary emigration	1.00 (0.00)	0.94 (0.06)	0.95 (0.05)	1.00 (NE)	0.41 (0.11)	0.05 (0.03)
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I. Random temporary emigration	1.00 (0.00)	0.97 (0.02)		0.97 (0.02)	0.41 (0.11)	0.05 (0.03)

Table 5. Continued.

River	Reach	Robust Design Model	N (SE), May	N (SE), June	N (SE), July	N (SE), August
Contentnea	1	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E=0, I=0 Classic robust design	226 (129)	411 (219)	349 (189)	287 (159)
Contentnea	1	$\hat{\phi}_{.}$, p.., $\hat{c}$.., N_t, E=0, I=0 Classic robust design	16 (5)	30 (9)	26 (8)	21 (7)
Contentnea	1	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, $E_{\cdot t}$, I. Markovian temporary emigration	14 (3)	27 (6)	22 (5)	18 (4)
Contentnea	1	**$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.** **Random temporary emigration**	**14 (3)**	**26 (6)**	**22 (5)**	**18 (4)**
Contentnea	2	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E = 0, I = 0 Classic robust design	410 (159)	190 (83)	308 (123)	58 (35)
Contentnea	2	$\hat{\phi}_{.}$, p.., $\hat{c}$.., N_t, E = 0, I = 0 Classic robust design	279 (282)	129 (133)	209 (213)	39 (44)
Contentnea	2	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, $E_{\cdot t}$, I. Markovian temporary emigration	31 (3)	14 (2)	23 (2)	4 (NE)
Contentnea	2	**$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.** **Random temporary emigration**	**31 (3)**	**14 (2)**	**23 (2)**	**4 (NE)**
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E=0, I=0 Classic robust design	322 (79)	199 (49)	169 (43)	138 (36)
NECFR	ALL	**$\hat{\phi}_{.}$, p.., $\hat{c}$.., N_t, E=0, I=0** **Classic robust design**	**9 (2)**	**5 (1)**	**4 (1)**	**4 (1)**
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, $E_{\cdot t}$, I. Markovian temporary emigration	9 (1)	16 (3)	13 (3)	11 (2)
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I. Random temporary emigration	9 (2)	5 (1)	4 (1)	4 (1)

Table 6. River, reach, model name, AIC_c value, delta AIC_c, AIC_c weight, and number of model parameters for random temporary emigration robust design models fit to data collected in 2002. Models were fit with and without empirical estimates of capture and recapture probability from radio-tagged fish. Bold indicates best-fit model with lowest AIC_c value and highest AIC_c weight.

River	Reach	Robust Design Model	AIC_c	Delta AIC_c	AIC_c Weight	Number of parameters
Contentnea	1	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.	8.45	1.04	0.31	7
Contentnea	1	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}$.., N_t, E. = I.	11.60	4.19	0.06	6
Contentnea	**1**	**$\hat{\phi}$ = 1, p.., $\hat{c}_{0.07}$, N_t, E. = I.**	**7.41**	**0.00**	**0.52**	**6**
Contentnea	1	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}_{0.07}$, N_t, E. = I.	10.64	3.22	0.10	5
Contentnea	**2**	**$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.**	**-52.68**	**0.00**	**0.92**	**6**
Contentnea	2	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}$.., N_t, E. = I.	-35.25	17.43	0.0002	6
Contentnea	2	$\hat{\phi}$ = 1, p.., $\hat{c}_{0.07}$, N_t, E. = I.	-47.85	4.83	0.08	6
Contentnea	2	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}_{0.07}$, N_t, E. = I.	-30.42	22.26	0.00001	5
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.	-9.27	2.56	0.20	7
NECFR	ALL	$\hat{\phi}$ = 1, $p_{0.04}$, $\hat{c}$.., N_t, E. = I.	-4.01	7.82	0.01	6
NECFR	**ALL**	**$\hat{\phi}$ = 1, p.., $\hat{c}_{0.04}$, N_t, E. = I.**	**-11.83**	**0.00**	**0.73**	**6**
NECFR	ALL	$\hat{\phi}$ = 1, $p_{0.04}$, $\hat{c}_{0.04}$, N_t, E. = I.	-6.46	5.37	0.05	5

Table 7. River name, sample reach, model name survival rate ($\hat{\phi}$ $\pm$ SE), emigration rate (G″ $\pm$ SE) between primary periods 1 and 2, emigration rate (G″ $\pm$ SE) between primary periods 2 and 3, capture probability ($\hat{p}$ $\pm$ SE), recapture probability ($\hat{c}$ $\pm$ SE), and population size per-km (N$\pm$ SE) for each primary period in 2002 using the random temporary emigration model with and without capture probability information from radio tags. Bold indicates best fit model (lowest AICc). Blanks indicate parameters that were not components of some models simulated. "NE" are non-estimable model parameters or standard errors that result from poor model fit due to sparse data.

River	Reach	Robust Design Model	Survival (SE)	G'' (SE) Periods 1-2	G'' (SE) Periods 2-3	$\hat{p}$ (SE)	$\hat{c}$ (SE)
Contentnea	1	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.	1.00 (0.00)	0.94 (0.03)	0.94 (0.03)	0.36 (0.11)	0.11 (0.04)
Contentnea	1	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}$.., N_t, E. = I.	1.00 (0.00)	0.77 (0.11)	0.77 (0.11)	0.07 (NE)	0.11 (0.04)
Contentnea	**1**	**$\hat{\phi}$ = 1, p.., $c_{0.07}$, N_t, E. = I.**	**1.00 (0.00)**	**0.94 (0.03)**	**0.94 (0.03)**	**0.36 (0.11)**	**0.07 (NE)**
Contentnea	1	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}_{0.07}$, N_t, E. = I.	1.00 (0.00)	0.77 (0.11)	0.77 (0.11)	0.07 (NE)	0.07 (NE)
Contentnea	**2**	**$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.**	**1.00 (0.00)**	**0.93 (0.02)**	**0.93 (0.02)**	**0.53 (0.08)**	**0.01 (0.01)**
Contentnea	2	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}$.., N_t, E. = I.	1.00 (0.00)	0.68 (0.11)	0.68 (0.11)	0.07 (NE)	0.01 (0.01)
Contentnea	2	$\hat{\phi}$ = 1, p.., $\hat{c}_{0.07}$, N_t, E. = I.	1.00 (0.00)	0.93 (0.02)	0.93 (0.02)	0.53 (0.08)	0.01 (0.01)
Contentnea	2	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}_{0.07}$, N_t, E. = I.	1.00 (0.00)	0.68 (0.11)	0.68 (0.11)	0.07 (NE)	0.07 (NE)
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$.., N_t, E. = I.	1.00 (0.00)	0.00 (0.00)		0.01 (0.01)	0.05 (0.03)
NECFR	ALL	$\hat{\phi}$ = 1, $p_{0.04}$, $\hat{c}$.., N_t, E. = I.	1.00 (0.00)	0.00 (0.00)		0.41 (0.11)	0.05 (0.03)
NECFR	**ALL**	**$\hat{\phi}$ = 1, p.., $\hat{c}_{0.04}$, N_t, E. = I.**	**1.00 (0.00)**	**0.94 (0.06)**	**0.95 (0.05)**	**0.41 (0.11)**	**0.05 (0.03)**
NECFR	ALL	$\hat{\phi}$ = 1, $p_{0.04}$, $\hat{c}_{0.04}$, N_t, E. = I.	1.00 (0.00)	0.97 (0.02)		0.41 (0.11)	0.05 (0.03)

Table 7. Continued.

River	Reach	Robust Design Model	N (SE), May	N (SE), June	N (SE), July	N (SE), August
Contentnea	1	$\hat{\phi}$ = 1, p.., $\hat{c}$ .., N_t, E. = I.	14 (3)	26 (6)	22 (5)	18 (3)
Contentnea	1	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}$ .., N_t, E. = I.	56 (15)	102 (21)	86 (19)	71 (17)
Contentnea	**1**	**$\hat{\phi}$ = 1, p.., $\hat{c}_{0.07}$, N_t, E. = I.**	**14 (3)**	**26 (6)**	**22 (5)**	**18 (3)**
Contentnea	1	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}_{0.07}$, N_t, E. = I.	56 (15)	102 (21)	86 (19)	71 (17)
Contentnea	**2**	**$\hat{\phi}$ = 1, p.., $\hat{c}$ .., N_t, E. = I.**	**31 (3)**	**14 (2)**	**23 (2)**	**4 (NE)**
Contentnea	2	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}$ .., N_t, E. = I.	143 (24)	66 (17)	107 (21)	20 (9)
Contentnea	2	$\hat{\phi}$ = 1, p.., $\hat{c}_{0.07}$, N_t, E. = I.	31 (3)	14 (2)	23 (2)	4 (NE)
Contentnea	2	$\hat{\phi}$ = 1, $p_{0.07}$, $\hat{c}_{0.07}$, N_t, E. = I.	143 (24)	66 (17)	107 (21)	20 (9)
NECFR	ALL	$\hat{\phi}$ = 1, p.., $\hat{c}$ .., N_t, E. = I.	9 (2)	5 (1)	4 (1)	4 (1)
NECFR	ALL	$\hat{\phi}$ = 1, $p_{0.04}$, $\hat{c}$ .., N_t, E. = I.	61 (12)	37 (6)	32 (9)	26 (8)
NECFR	**ALL**	**$\hat{\phi}$ = 1, p.., $\hat{c}_{0.04}$, N_t, E. = I.**	**9 (2)**	**5 (1)**	**4 (1)**	**4 (1)**
NECFR	ALL	$\hat{\phi}$ = 1, $p_{0.04}$, $\hat{c}_{0.04}$, N_t, E. = I.	61 (12)	37 (10)	32 (9)	26 (8)

Table 8. Flathead catfish population biomass and density with associated standard error and approximate 95% confidence intervals (±2 SE) estimated for each river, reach, and month. Estimates were made using the best population estimate for each reach (see text) and average flathead catfish weights for that month of sampling.

Year	River	Reach	Month	Biomass (kg/km)	SE	95% Confidence interval	Biomass (kg/ha)	SE	95% Confidence interval	Density (N/km)	SE	95% Confidence interval	Density (N/ha)	SE	95% Confidence interval
2002	Contentnea	1	May	38.4	37.5	0 – 113.4	12.4	21.3	0 – 66.8	14	3	8 – 20	5	1.7	1.1 – 7.9
2002	Contentnea	1	June	54.9	72.0	0 – 198.9	17.8	41.0	0 – 126.9	26	6	14 – 38	8	3.4	1.6 – 15.2
2002	Contentnea	1	July	46.0	57.4	0 – 160.8	14.9	32.6	0 – 99.9	22	5	12 – 32	7	2.8	1.4 – 12.8
2002	Contentnea	1	August	21.8	31.9	0 – 85.6	7.1	18.2	0 – 49.9	18	3	10 – 26	6	2.3	1.3 – 10.4
2002	Contentnea	2	May	65.7	60.05	0 – 185.8	5.0	16.6	0 – 43.5	31	3	25 – 37	2	0.8	0.7 – 4.0
2002	Contentnea	2	June	21.7	31.3	0 – 84.3	1.7	8.7	0 – 20.1	14	2	10 – 18	1	0.6	0 – 2.2
2002	Contentnea	2	July	35.0	44.33	0 – 123.6	2.7	12.3	0 – 28.6	23	2	18 – 26	2	0.6	0.6 – 2.8
2002	Contentnea	2	August	5.6	NE	NE	0.4	NE	0 – 4.4	4	NE	NE	0.3	NE	NE
2002	NECFR	All	May	7.5	12.3	0 – 32.2	0.7	3.7	0 – 9.2	9	0.8	0 – 19	2	1.5	0 – 3.8
2002	NECFR	All	June	1.8	3.6	0 – 8.9	0.2	1.1	0 – 2.4	5	0.5	0 – 11	1	0.9	0 – 2.3
2002	NECFR	All	July	3.5	4.7	0 – 12.9	0.3	1.4	0 – 3.6	4	0.4	0 – 10	1	0.9	0 – 2.2
2002	NECFR	All	August	2.3	3.3	0 – 90.	0.2	1.0	0 – 2.4	4	0.3	0 – 8	1	0.6	0 – 1.5

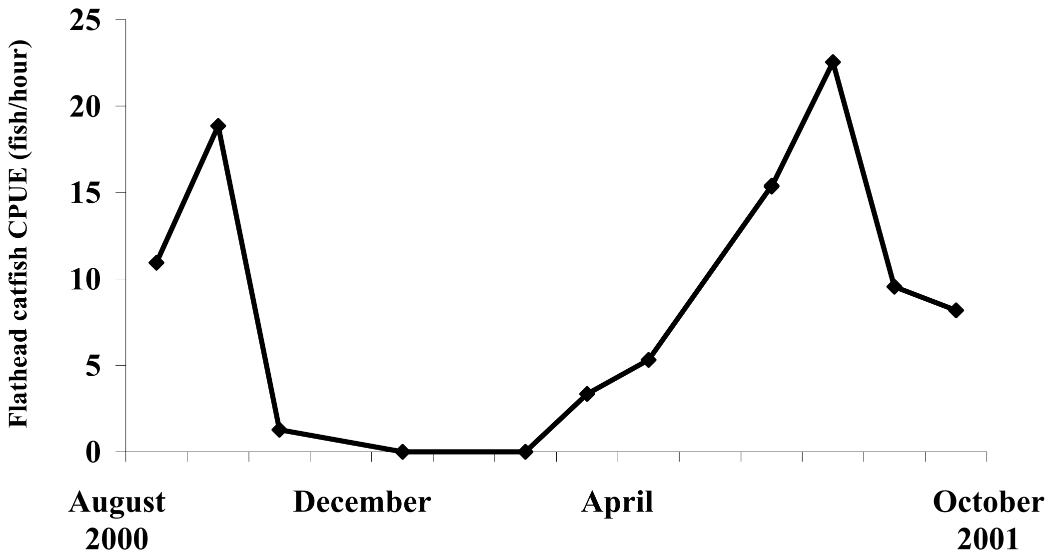


Figure 1. Seasonal CPUE (number of fish / hour) for reach 1 in Contentnea Creek during sampling in 2000 and 2001.

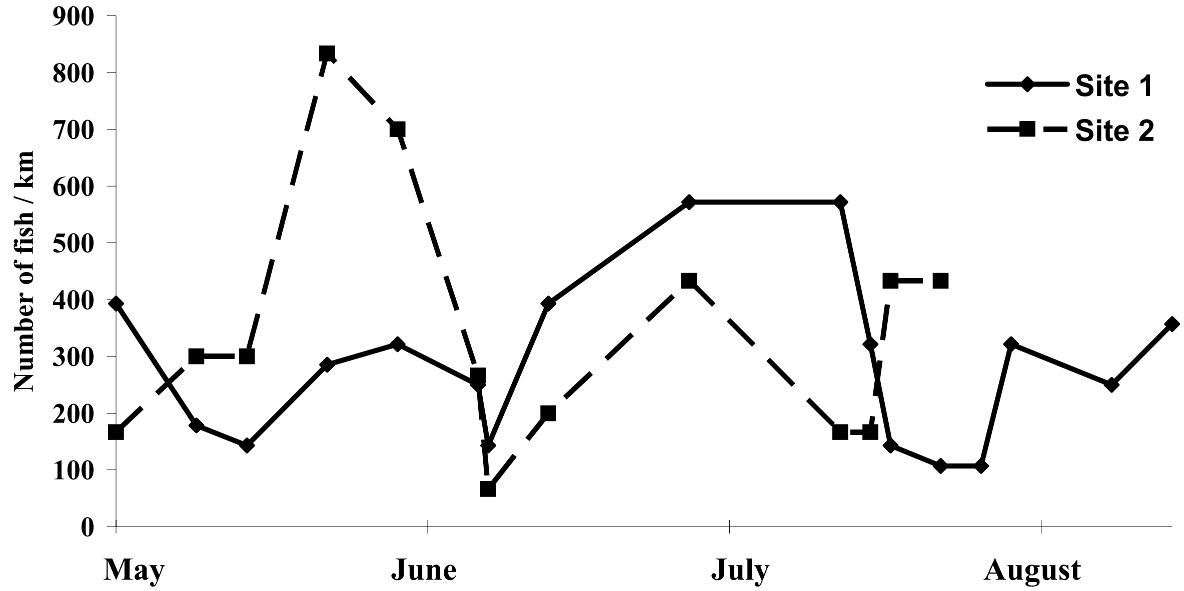
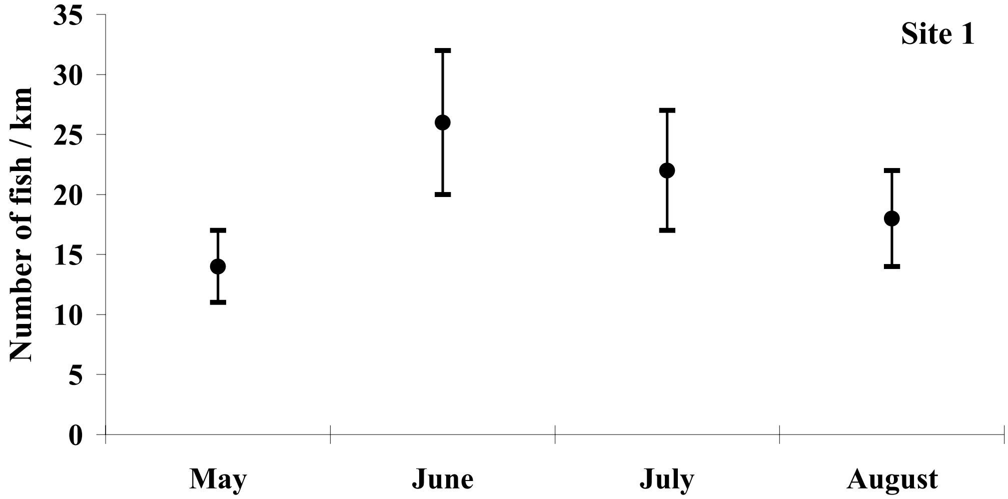


Figure 2. Open population model estimates for reach 1 and reach 2 in Contentnea Creek during 2001. Population estimates are biased by temporary emigration although population trends may be accurate (see text).



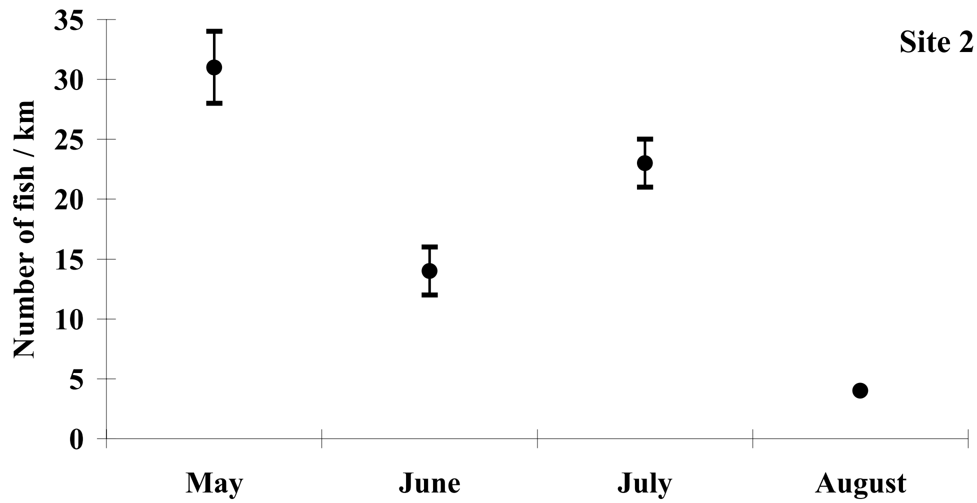


Figure 3. Estimated population size (± SE) for each sample reach during each primary period from Contentnea Creek during 2002 using the best fit model (see text), a robust design model with random temporary emigration.

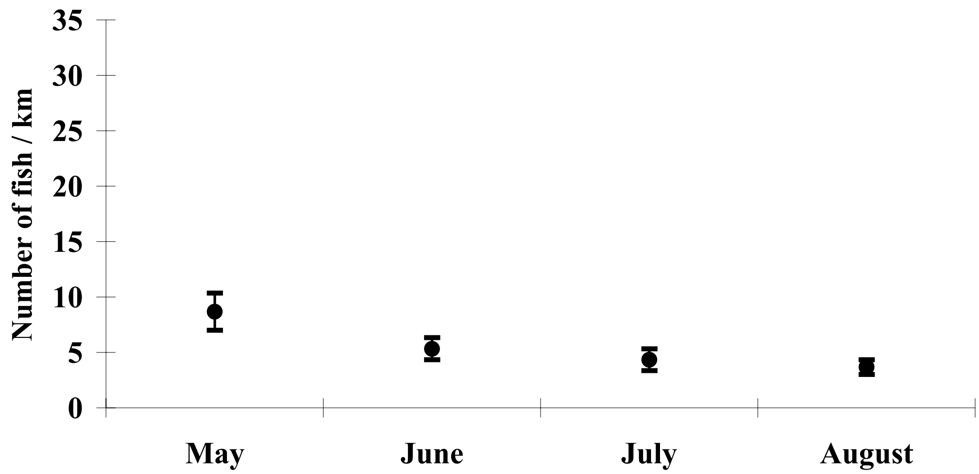


Figure 4. Estimated population ($\pm$ SE) size of sample reach during each primary period from the Northeast Cape Fear River during 2002 using the best fit model (see text), a classic robust design model with fixed survival.

CHAPTER 4

FOOD HABITS OF INTRODUCED FLATHEAD CATFISH

Abstract

I found that in three North Carolina coastal rivers (Contentnea Creek, Northeast Cape Fear River, Lumber River), over two years, flathead catfish fed on a wide variety of freshwater fish and invertebrates, anadromous fish, and occasionally estuarine fish and invertebrates. Fish or crayfish comprised more than 50% of the stomach contents by percent occurrence, percent-by-number, and percent-by-weight in all rivers and years. A significant difference in the diet composition percent-by-number was found between Contentnea Creek and the Northeast Cape Fear River ($p < 0.0001$). Significant differences were not found between years within Contentnea Creek ($p = 0.32$) but were found within the Northeast Cape Fear River ($p = 0.009$). Feeding intensity (as measured by stomach fullness) was highest in the Northeast Cape Fear River and was associated with a lower mean size of feeding flathead catfish in this river than in those in Contentnea Creek or the Lumber River. This may be because of an allometric bias in the stomach fullness index used which does not account for small fish having a proportionally larger stomach size : fish body size ratio than large fish. A significant correlation between diet item length and flathead catfish total length was found for Contentnea Creek in 2001 ($R = 0.221$, $p = 0.006$) but not in 2002 ($R = -0.053$, $p = 0.435$). This relationship was not significant in the Northeast Cape Fear River in either year (2001 $R = 0.15$, $p = 0.24$; 2002 $R = -0.05$, $p = 0.67$). Based on the diet composition data collected in this study and those published on native and introduced flathead catfish populations, I am not able to support or refute the hypothesis that flathead catfish are preferentially feeding on specific species or families. However, the flathead catfish populations examined here are well established, and the greatest impact from selective predation may have occurred immediately following introduction. Based on my findings, flathead catfish could restructure

or suppress native fish communities in coastal rivers through direct predation because of their primarily piscivorous food habits.

Introduction

The flathead catfish *Pylodictis olivaris* is a large piscivorous catfish native to the Rio Grande, Mississippi, and Mobile river drainages (Smith-Vaniz 1968; Jenkins and Burkhead 1994) and has been introduced by legal and illegal means into at least 13 states and one Canadian province (Jackson 1999). The only known flathead catfish introduction into North Carolina waters occurred in 1966 when 11 adults (total weight 107 kg) were released into the Cape Fear River near Fayetteville, North Carolina (Guier et al. 1981). Within 15 years the flathead catfish distribution had expanded to cover a 200-km section of the river, and it had emerged as the dominant predator within the Cape Fear River system (Guier et al. 1981).

Flathead catfish demonstrate high individual and population growth rates (Guier et al. 1981; Quinn 1989; Munger et al. 1994; Nash and Irwin 1999), rapid dispersal (Guier et al. 1981; Ashley and Buff 1987; Jenkins and Burkhead 1994), and carnivorous food habits (Swingle 1967; Quinn 1989; Ashley and Buff 1987). Individual flathead catfish growth rates in introduced populations are generally higher than those in native riverine systems, but are similar to those reported in reservoirs (Guier et al. 1981; Quinn 1989; Munger et al. 1994). Maximum size of flathead catfish in North Carolina (from angling records) is currently 56% of the world record collected in Kansas (31.8 kg NC; 56.4 kg KS).

Throughout their introduced range, feeding patterns of flathead catfish have been widely studied to discern their impact on native fish communities. Swingle (1967) documented that flathead catfish >254-mm TL "may compete with fishermen for fish of harvestable size" in ponds. Results from studies such as those of Swingle (1967), as well as widespread angler concern over declining populations of native sport fishes following flathead catfish introductions, have led several state agencies to study flathead catfish food habits in the fish's introduced range. Several of these studies generally suggest a decline in native fish populations following introduction of flathead catfish (Guier et al. 1981; Thomas 1995) while others detected no impact on native fisheries following introduction (Ashley and Buff 1987; Quinn 1987).

Information on native fish community composition prior to invasion is usually limited for any given area, and introduced species introductions often occur simultaneously with other anthropogenic impacts that may alter native fish abundance (Townsend and Crowl 1991; White and Harvey 2001). This phenomenon often results in a time-series bias, where the present fish assemblage suffers from the "ghost of predation past" (i.e., the impact resulting from predation pressure that occurred in the past remains evident) such that any potential impact on native species by the introduced species occurred prior to the study. Further, it may be assumed that declines in native species are the result of species (i.e., flathead catfish) introduction, when it is also possible that a suite of biotic (e.g., poor recruitment) or anthropogenic abiotic changes could alter fish assemblage composition (Williamson 1997; White and Harvey 2001).

In this chapter, I examine diet patterns in introduced populations of flathead catfish from three coastal river systems in North Carolina and compare these results to published foraging information for native and other introduced flathead catfish populations. It is widely thought that invasive species, at least initially, exploit an abundance of prey types that did not co-evolve with the mode of predation by the invader (Moyle and Light 1996a, b). I attempt to ascertain if foraging patterns exist that fit current conceptual models of invasive species foraging theory to address this question: do introduced flathead catfish selectively feed on prey types that are not present in their native range? I examine this theory through comparative analysis of flathead catfish prey items from this and other studies.

Methods

Study Sites

Three rivers of similar size (mean width ~50 m each river) and drainage basin area (Northeast Cape Fear River, Cape Fear River drainage 24,144 km^2; Contentnea Creek, Neuse River drainage 16,149 km^2; Lumber River, Yadkin-Pee Dee River drainage 18,702 km^2) located in the coastal plain region of eastern North Carolina were selected with assistance from North Carolina Wildlife Resources Commission (NCWRC) biologists. Flathead catfish presence in each of these rivers had been documented by routine sampling as part of a long-term fish community monitoring conducted by the NCWRC. I conducted intensive sampling in fixed sample reaches spanning long-term NCWRC sampling locations. Two, 1-km reaches were sampled in both Contentnea Creek and the Lumber River, and 3, 1-km reaches were sampled in the Northeast Cape Fear River.

Field and Lab Procedures

Flathead catfish were collected using low-frequency electrofishing (Smith-Root INC. Mark VI GPP unit pulsed-DC current, 1.5-2.0 amps, 15-pps), a non-lethal capture technique that has been shown to be the most effective collection technique for flathead catfish (Justus 1996; Stauffer and Koenen 1999). Fish were collected when water temperatures exceeded 18°C (generally May-September), the minimum temperature threshold to efficiently capture flathead catfish in North Carolina (Chapter 3). All flathead catfish collected were weighed (g) and measured (TL mm). I used pulsed gastric levage (PGL) to collect diet samples. This technique is shown to be a highly effective non-lethal technique for removing stomach contents from flathead catfish (>95% effective, Waters et al. 2003). Stomach contents were individually labeled, sealed, and placed on wet ice. All extracted diet materials were returned to the laboratory and frozen. Prior to analysis samples were thawed, and extracted stomach contents identified to the lowest possible taxon, blotted and weighed wet (± 0.01 g), then measured along the longest axis (± 0.5 mm). Items that were not identifiable to family (e.g., a few bones, scales, or pieces of tissue) were grouped as either unidentified fish or unidentified invertebrates.

Stomach contents were quantified using several standard techniques (Bowen 1996). The frequency of occurrence of prey items was measured by compiling a cumulative list of all of the families found in the stomach contents. I then recorded the presence or absence of each stomach item from the list for each fish. For example, if 23 of the 84 flathead catfish stomachs with contents examined in Contentnea Creek during 2002 contained the family Cambaridae, then the frequency of occurrence of Cambaridae was 0.27 or 27%.

I also examined the percent composition by number of stomach contents for individual fish by calculating the percent composition of each prey group in the flathead catfish stomachs, and then calculating a mean percent composition value for each group in each year and river. I then pooled the samples for each year by river and used a repeated measures multivariate analysis of variance (MANOVA) to compare diet composition by number between rivers (years combined) and between years within each river. In this comparison, the treatment was river or year, the repeatedly measured response variable was percent by number of each prey group in the stomach contents, and the replicates were individual fish within each river. The Lumber River was not included in this analysis because of low sample sizes.

Stomach fullness was calculated ([stomach contents wet weight/fish wet body weight] x 100) as a measure of feeding intensity and reported as a percent of the flathead catfish weight. Correlations between stomach item length and fish TL were examined for trends in prey size and fish size in each river and year. Percent composition by weight of stomach contents was summed across all flathead catfish prey items in each year and river and presented as mean weights of each prey group by year and river.

Results

Most stomach items were highly digested and often difficult to identify. Identification to the family level was common and each family was considered a group for analysis (Table 1). Flathead catfish have a well developed jaw and pharyngeal teeth, which masticated many of the food items when eaten. Unidentifiable material in the stomach contents was classified as unidentified fish or unidentified invertebrates and included as a group (similar to family) for analysis. Typical unidentified contents included pieces of fish flesh, scales, bones, or spine fragments. Unidentified invertebrates were usually pieces of insect wing, thorax, or legs.

Contentnea Creek

Flathead catfish in Contentnea Creek were primarily piscivorous with fish comprising the majority of stomach contents by frequency of occurrence, percent by number, and weight each year (Tables 2-4). In 2001, stomach contents from 176 fish were examined, of which 80 contained food items (45%) from 7 identifiable fish families and 4 invertebrate families. In 2002, contents from 158 stomachs were examined, and 84 contained food items (53%) from 6 fish families and 5 invertebrate families. Unidentifed fish material was the most common prey item by occurrence (57.5%) and number (49.0%) (Tables 2 and 3), but the group Centrarchidae (mostly *Lepomis spp.*, “sunfish”) was the most common item by weight (48.2%, Table 4). On average, individual prey items from the group Percidae (perch and darters) were the largest by weight (Table 5, mean = 28.5 g), although this average was heavily skewed by one large yellow perch *Perca flavescens* (168 g). If this yellow perch was not included, the group Centrarchidae would be the largest by weight. Similar results were found in 2002 for frequency of occurrence (Table 1, unidentified fish = 45.4%), percent-by-number (Table 2, unidentifiable fish = 45.39%), and percent total weight (Table 3, unidentifiable fish = 48.2%, Tables 1-3). Sunfish were the heaviest individual prey item (Table 4, mean = 14.5 g). The group Cambaridae (crayfish) was also a common prey item by occurrence, number, and total weight (Tables 2, 3). In 2001, crayfish ranked second in both occurrence (Table 2, 26.3%) and number (Table 3, 18.7%) and were fourth in weight (Table 4, 3.91%). In 2002, crayfish were again the second most commonly occurring stomach item (Table 2, 19.3%), the third most common item by number (Table 3, 13.6%) and by total weight (Table 4, 10.1%). Diet percent composition was not significantly different between years (Wilks’ Lambda $F_{14,149} = 1.16$, $p = 0.32$). Feeding intensity as measured by stomach fullness was low (<1.0 % of flathead catfish body weight) and variable during 2001 and 2002 in Contentnea Creek (Table 6). The relationship between flathead catfish total length and diet item length was significant in 2001 ($R = 0.22$, $p = 0.006$, Figure 1) but was not significant in 2002 ($R = -0.05$, $p = 0.43$, Figure 1).

Northeast Cape Fear River

Stomachs of flathead catfish from the Northeast Cape Fear contained primarily crayfish and fish material from unknown families. In 2001, stomach contents from 100 flathead catfish were examined, of which 29 contained food items (29.0%) from 3 identifiable fish and 4 invertebrate families. In 2002 contents from 115 stomachs were examined, and 58 contained food items (50.4%) from 2 identifiable fish and 3 invertebrate families. In 2001, unidentified fish material was the most common prey item by occurrence (Table 2, 55.2%) and number (Table 3, 38.8%), but sunfish were the most common item by total weight (Table 4, 45.9%). Sunfish were also the largest prey item by weight (Table 5, mean = 9.49 g). In 2002, crayfish were the leading stomach item by frequency of occurrence (Table 2, crayfish = 60.3%), number (Table 3, crayfish = 53.4%), and percent total weight (Table 4, crayfish = 52.4%). Sunfish were the largest prey group by average weight (Table 5, mean = 8.08 g). Overall in 2001, all fish material comprised about 50% of the stomach contents by occurrence, number, and total weight, while invertebrates (primarily crayfish) were the dominant items in 2002. Diet percent composition was significantly different between years (MANOVA Wilks' Lambda $F_{9, 77} = 2.68$, $p = 0.009$). Feeding intensity in the Northeast Cape Fear River was also low (stomach fullness range 0.2 - 3.8%) and variable during 2001 and 2002 (Table 6). No correlation was detected between flathead catfish total length and stomach item length in 2001 ($R = 0.15$, $p = 0.24$, Figure 1) or 2002 ($R = -0.45$, $p = 0.67$, Figure 1).

Lumber River

Flathead catfish catch rates in the Lumber River were low (Chapter 3) which reduced sample sizes for diet analyses and eliminated the Lumber River from some analyses. In 2001, stomach contents from 23 fish were analyzed, and 7 of these contained prey items (30.4%) from 1 identifiable fish and 1 invertebrate group. In 2002, 24 stomachs were analyzed, and 15 contained prey items (62.5%) from 2 identifiable fish and 2 invertebrate families. As in the other rivers, stomach contents were primarily composed of unidentified fish remains and crayfish. Unidentified fish were the most common stomach item in 2001 by occurrence (Table 2, 57.1%) and number (Table 3, 47.6%) while sunfish were the most common group by weight (Table 4, 51.8%) and the largest group by mean weight (0.66 g). In 2002, unidentified fish were the most common group by occurrence (Table 2, 60.0%), while crayfish were the most common group by number (Table 3, 48.1%), and Ictaluridae (catfish) by weight (Table 4, 55.8%). Ictalurids were also the largest item by mean weight (Table 5, mean = 27.9 g). Feeding intensity in the Lumber River was low (Table 6, stomach fullness range 0.0001 - 0.95 %).

Summary and Between Year and River Comparison

Diet percent composition between Contentnea Creek and the Northeast Cape Fear River was significantly different (MANOVA Wilks' Lambda $F_{15, 245} = 4.71$, $p < 0.0001$). Because of low sample sizes, the Lumber River was not included in this comparison. The percent-by-number data show that the two most common food types were either unidentified fish material (4 of 6 estimates) or crayfish (2 of 6 estimates). The results from the percent-by-number results correspond well with the frequency of occurrence results; most flathead catfish are consuming other fish in their diet (Table 3), and the most commonly occurring prey items were fish material. Fish material comprised >50% of all stomach items in 5 of the 6 estimates. The MANOVA results between years within each river are clearly supported by closely examining the frequency-by-number data. In Contentnea Creek, the ranked composition of the diet material by number did not change between 2001 and 2002 (Table 3) and the MANOVA test for differences in percent-by-number of each group was not significant ($p = 0.32$). However, in the Northeast Cape Fear River, the rankings of the diet composition changed fairly dramatically between years from unidentified fish as the leading group with about 39% of the total diet to crayfish as number one in 2002 with about 53% of the diet (Table 3). As a result of this change, the MANOVA between 2001 and 2002 was significant ($p = 0.009$).

Discussion

Identification of stomach contents may be difficult due to digestion of the prey item between the time it is consumed by the predator and sampled by the researcher (Bowen 1996). I found a high frequency of empty stomachs, low stomach fullness values, and highly digested condition of most stomach contents that made identification below the family level difficult. This also biased my assessment of the actual length or weight of a prey item towards an underestimate. Bowen (1996) recommended collecting fish for diet analysis when their stomachs are at the fullest. Minckley and Deacon (1959) found the highest average number of organisms in flathead catfish stomachs in fish collected between 6:30 a.m. and 12:30 p.m., which includes the time period I collected most of my samples. Bowen (1996) also cautioned that some capture gears may cause fish to regurgitate their stomach contents. I used low frequency electrofishing to collect my fish and occasionally noticed some regurgitation of food while fish were being held in the live-well prior to processing. However, the amount of regurgitated material observed was low, and I attempted to minimize collection stress and process collected fish as rapidly as possible to minimize regurgitation.

My frequency of occurrence data (Table 2), clearly demonstrate that more than 50% of flathead catfish consume other fish. In 5 of 6 estimates (3 rivers x 2 years), other fish (identified families + unidentified fish) were found in more than 85% of the flathead catfish stomachs with food items. Of the identified fish families, sunfish frequently occurred in each river and year and were found in the top 3 in occurrence ranking in 4 of the 6 estimates (Table 2).

Crayfish occurrence ranked either first or second in all estimates. Invertebrates were found in less than 50% of flathead catfish stomachs in 5 of the 6 estimates. Six other invertebrate families were identified in stomach contents, but occurrences of these families were rare. Surprisingly, juvenile marine shrimp (Penaidae, most likely white shrimp *Litopenaeus setiferus*) were found in about 7% of the flathead catfish stomachs in Contentnea Creek but were not found in stomach contents from the other rivers. It is not clear where flathead catfish encountered these prey items, because Contentnea Creek is about 25 km from the beginning of the Neuse River estuary, the closest known white shrimp habitat. As soft-bodied invertebrates, the digestion rate of shrimp would be rapid (Bowen 1996). It is highly unlikely that a flathead catfish consuming shrimp in the estuary and then swimming the 25-km to Contentnea Creek would not fully digested these items. Flathead catfish must be encountering white shrimp much closer then the Neuse River estuary, perhaps within the mainstem Neuse River via a counter-current river flow which may be transporting small marine invertebrates up river. The use of marine derived food items by flathead catfish is discussed in more detail below and warrants further investigation.

The percent-by-weight data were not compiled on an individual fish level, but were instead pooled by river and year because the condition of the stomach items was more conducive to assessing prey size from length that weight. For example, a complete fish spine in the stomach contents provided an adequate estimate of the minimum length of the fish prey eaten, but it would not provide a good indicator of the weight of the prey item. Unidentified fish or crayfish were usually the leading prey groups from the frequency of occurrence (Table 2) and the percent-by-number analysis (Table 3). When I examine the overall contribution of the various prey groups by weight (Table 4), fish material again contributes more than 70% of the diet by weight in 5 of the 6 estimates and it usually (4 of 5) contributes more than 85% of the diet by weight. This is further evidence that fish provides most of the food items to flathead catfish. The largest prey groups by weight are usually in the family Centrarchidae, Percidae, and Ictaluridae based on the percent-by-weight data and the mean weight of prey items data (Table 5). Although crayfish often ranked first or second by occurrence and frequency, by percent weight and average weight they usually ranked third or forth (Tables 4, 5).

Because most stomach contents were highly digested, feeding intensity as measured by stomach fullness was often < 1.0 (Table 7). In seven of the nine month x year x river combinations when more than one estimate of stomach fullness was available for each river, the Northeast Cape Fear River had the highest stomach fullness values of the three rivers (Table 6). In these seven instances, the mean size of the flathead catfish with stomach contents was lower in the Northeast Cape Fear than the other rivers (Table 6). These results are likely because of an allometric bias in the stomach fullness index used, which has been documented for several fish species across a range of sizes (Kwak et al. 1992) where the stomach size : fish size ratio is larger for small fish. This could also indicate that smaller fish may be feeding more intensively than larger fish. Weight- specific metabolic demands increase with decreasing size (Diana 1995). Also, as fish grow larger they may switch prey types or sizes of prey (Werner and Hall 1974). A combination of either of these could be occurring with flathead catfish in these rivers and affecting estimates of feeding intensity. Differential feeding intensity by size classes of flathead catfish should be explored further.

Often as predator size increases, prey size increases to a certain level until predators begin to make choices related to prey availability, handling time, and energy value of the prey (Diana 1995). This is likely true for flathead catfish. However, I found few large prey items in the stomach contents although there was indications from some items (such as large scales) from larger flathead catfish that came from large prey items.

Flathead catfish stomachs from Contentnea Creek contained twice as many identifiable fish families as did those from the Northeast Cape Fear River. Although the comparison between Contentnea Creek and the Lumber River was not performed due to low numbers of stomach samples from the Lumber River, flathead catfish from Contentnea Creek had six times as many identifiable fish families as did flathead catfish in the Lumber River. Of the 16 prey groups considered here (14 identifiable prey families, 2 unidentifiable groups) only six were common between the Northeast Cape Fear River and Contentnea Creek in 2001 and 2002, and of these six, two were the unidentified fish and invertebrate groups. The MANOVA result also serves as supporting evidence for the ecological conclusion that flathead catfish in Contentnea Creek fed on a wider range of prey types than in the Northeast Cape Fear River. Although not supported by a statistic, the same conclusion is apparent between the Lumber River and Contentnea Creek (Tables 2, 3); flathead catfish fed on a wider range of prey types in Contentena Creek.

My results are similar to an early study describing flathead catfish feeding patterns (Minckley and Deacon 1959) who found that the "Kinds [sic] of foods eaten {by flathead catfish} evidently depended on its [sic] availability." Similar to findings in native systems (Layher and Bloes 1980; Roell and Orth 1992), crayfish were also commonly consumed by flathead catfish in my study (Tables 2-3). Roell and Orth (1992) estimated that flathead catfish consumed 10% of the annual production of age-1 and age-2 crayfish in the New River, West Virginia. The frequency of crayfish occurrence in flathead stomachs may be somewhat biased by the slow digestion rate of the hard crayfish exoskeleton. Bowen (1996) cautioned that slowly digested prey items may accumulate in the digestive system of a predator relative to more rapidly digested items. Even if crayfish remains accumulated in the digestive tract of flathead catfish and positively biased crayfish abundance in the diet, they are still likely an important component of flathead catfish diet.

Juvenile anadromous shad were found in flathead catfish stomachs in Contentnea Creek (Tables 1-3). As part of other fisheries research sampling efforts within the Neuse River basin, flathead catfish were incidentally collected and found to be feeding on adult hickory shad *Alosa mediocris* (J. Hightower, North Carolina State University *unpublished data*). Ashley and Buff (1987) also found adult anadromous shad in flathead stomachs from the Cape Fear River, North Carolina. Adult shad were not present in the rivers I sampled during the time periods I could effectively collect flathead catfish. Within their native and introduced range flathead catfish have been documented to forage heavily on juvenile and adult gizzard shad *Dorosoma cepedianum* (Layer and Bloes 1980; Quinn 1987). This further indicates that adult clupeids do not pose gape limitations to adult flathead catfish. The impacts of flathead catfish predation on juvenile and adult anadromous shad could be important to managers involved with anadromous shad restoration efforts along the Atlantic slope. This is explored further in Chapter 5.

The overall contribution of marine-derived prey items to flathead catfish diets in this study (i.e., shrimp, hogchokers *Trinectes maculatus*, and anadromous shad) is relatively low (Tables 1-3) but potentially ecologically important. MacAvoy et al. (2000) examined the use of marine derived nutrients by blue catfish *Ictalurus furcatus*, an introduced omnivore in the James River, Virginia using stable isotope techniques. These authors found that introduced blue catfish derived a significant proportion of their nutrition from spawning anadromous

Alosa spp. (MacAvoy et al. 2001) and suggested that the impact of introduced piscivores along the Atlantic coast be examined.

Comparisons among flathead catfish diet studies

Prey species are thought to be unusually vulnerable to the predation style of a newly introduced predator (Williamson 1996; Moyle and Light 1996a). Guier et al. (1981) reported large abundance changes (by change in percent composition by weight of total population biomass) in the native fish community in the Cape Fear River, North Carolina following flathead catfish introduction. The largest changes were found in the native ictalurids, primarily brown bullheads *Ameiurus nebulosus* and flat bullheads *Ictalurus platycephalus*. Bluegill *Lepomis macrochirus*, black crappie *Pomoxis nigromaculatus,* and blue catfish were the most frequently occurring items found in flathead catfish stomachs by Guier et al. 1981 (and all of these species were found in samples from my study). Ashley and Buff (1986) in a follow-up study to that of Guier et al. (1981) found that "…there is no evidence to support anglers' claims that flathead catfish may be responsible for the reputed decline in sunfish populations…." Moser and Roberts (1999) did not collect any native ictalurids in river reaches to examine the effects of introduced ictalurids and recreational electrofishing on ictalurid populations in the Cape Fear River. It is possible that flathead catfish and blue catfish extirpated native ictalurids in the section of the Cape Fear studied by Moser and Roberts (1999). Ashley and Rachels (1998) noted a decline in electrofishing catch rates for native red breast sunfish in the Black and Lumber rivers, North Carolina, and considered predation by flathead catfish as a possible reason for this decline.

Quinn (1987) examined diet patterns in the introduced flathead catfish population in the Flint River, Georgia and suggested, "…adverse impacts on traditional fisheries are unlikely," based on findings that small flathead catfish fed primarily on crayfish and darters (*Etheostoma spp.*), and larger flatheads fed on gizzard shad *Dorosoma cepedianum*, sunfish (*Lepomis spp.*), and suckers (Catostomidae). In the Altamaha River, Georgia, Thomas (1995) documented an 80% decline in redbreast sunfish abundance and near elimination of native bullheads following flathead catfish introduction. Over the same time period, electrofishing catch rates for flathead catfish increased nearly 400%. This led Thomas (1995) to implicate flathead catfish as the cause for changes in the Altamaha River's fish assemblage. In other lotic systems with introduced flathead populations such as the Ocmulgee River, Georgia, abundances of silver redhorse *Moxostoma anisurum*, robust redhorse *M. robustum*, snail bullhead *Ameiurus brunneus*, flat bullhead, and redbreast sunfish were all negatively correlated with flathead catfish presence and abundance likely due to direct predation by flathead catfish (Bart et al. 1994). Silver redhorse is the only species of this group found in the native range of flathead catfish.

Flathead catfish may be contributing to the decline of the federally threatened Gulf sturgeon *Acipenser oxyrinchus desotoi* in the Apalachicola River, Florida by consuming young sturgeon (Fuller et al. 1999). Flathead catfish are not native to the Apalachicola River, but flathead catfish and Gulf sturgeon distributions overlap in rivers west of Mobile Bay (i.e., Pearl River, Mississippi). Flathead catfish are also thought to be contributing to the decline of the federally endangered razorback sucker *Xyrauchen texanus* in the San Pedro River, Arizona, due to intensive predation on juveniles, and are likely to prevent re-establishment of this species in its native range (Marsh and Brooks 1989). Fuller et al. (1999) considered the introduction of flathead catfish as probably the most biologically harmful of all fish introductions in North America.

My results correspond well with general trends from a range of published studies examining flathead catfish feeding patterns. Juvenile flathead catfish generally prey intensively on invertebrates when small, and then feed on progressively larger prey items (mostly fish) as they grow larger (Minckley and Deacon 1959). These results are similar, and based on my findings and other published studies, it appears that flathead catfish are obligate carnivores that prefer fish prey.

When I examine the few piscine prey items identifiable in my study to species from all the rivers combined, flathead catfish preyed both on species which co-evolved with them and species which did not. The paradigm that introduced predators selectively feed on prey species unfamiliar with a particular predation style is not strongly supported or refuted from my diet information alone, or by the published information on flathead catfish diets (see above). Indirect evidence demonstrating a correlation in declines of specific prey species with the introduction of flathead catfish found in other studies supports the hypothesis that flatheads may affect certain species or families. Direct evidence of flathead catfish selectively feeding on a prey species may be difficult to ascertain given the variety of animal prey items and the difficulty I encountered in identifying stomach contents. However, the impact of the additional predation pressure from flathead catfish, even at low levels, may exceed the sustainable mortality level for a particular prey species population; a modeling exercise may further resolve this hypothesis (Chapter 5).

In both Contentnea Creek and the Northeast Cape Fear River, flathead catfish have a broader range of available forage items, including anadromous and estuarine species, than those in the Lumber River. These species may serve as a predation buffer to resident native freshwater fishes by diffusing flathead catfish predation pressure across a larger prey base.

This finding supports the suggestion by Ashley and Rachels (1998) that declines in native redbreast sunfish (which did not co-evolve with flathead catfish) populations observed in the Lumber River may be a result of direct predation by flathead catfish, because fewer potential prey types are available in the Lumber River than in the other rivers I examined.

Future work

Quantitative evaluation of prey selectivity by flathead catfish would provide clearer insight into whether flathead catfish selectively prey on certain species or families. However, this evaluation is difficult to accomplish, not only because of the limitations in readily identifying stomach contents I observed, but other logistic reasons as well. I was able to estimate the relative proportion of prey items in the stomach contents, yet it is much more difficult to define the relative abundance of prey items that were available as prey to flathead catfish. Ideally, prey abundance estimates would need to be quantified simultaneously with flathead catfish diet samples. Even if the abundance of potential prey items was quantified with the diet samples, this does not necessarily describe the abundance of prey organisms encountered by feeding flathead catfish. Diurnal monitoring of radio-tagged flathead catfish would provide insight into the habitat types flathead catfish are most active in, possibly providing insight into the habitat areas and times that should be sampled to evaluate what prey are available to flathead catfish while they are feeding. Some salmonids are known to feed on invertebrates during the nighttime invertebrate drift and shift to feeding on fish during the day (Bowen 1996). The flathead catfish diet composition in this study may be similarly diurnal, with flathead catfish feeding at night on crayfish (when crayfish are emergent from burrows) and on other fish either at night or during the day. A diel comparison of stomach samples from several 24-hour sampling periods may help answer this question.

The use of marine prey items by flathead catfish is an important area of research that should be explored. Comparative stable isotope studies of flathead catfish isotopic signatures in areas accessible to estuarine environments and in areas separated from marine environments (e.g., above dams) would provide insight into the extent of use of marine-derived resources. Sonic telemetry of flathead catfish in areas adjacent to estuarine environments coupled with diet sampling as in my study could provide information on the extent of estuarine habitat use and feeding by flathead catfish. This result is particularly important to resource managers concerned with anadromous fish stocks and in managing marine species that use estuarine environments as nursery areas where juveniles may be susceptible to flathead catfish predation.

Conclusions and management implications

I have shown that introduced flathead catfish in coastal North Carolina are primarily piscivorous and feed on a wide variety of fish families. Flathead catfish also frequently consume crayfish, another important component of their diet. Many of the fish families I found in the flathead catfish diet contain species that represent important recreational fisheries in coastal North Carolina rivers such as bluegill sunfish, largemouth bass, red breast sunfish, and anadromous shad. Other families represented in the diet contain species of special concern due to their imperiled population status. Based on the findings of this study and from reviewing published flathead catfish food habits papers, I am not able to clearly confirm or refute the hypothesis that flathead catfish selectively feed on certain prey species including recreationally important sportfishes or species which did not co-evolve with flathead catfish. However, the flathead catfish populations examined here are established, reproducing populations, and if selective feeding by flathead catfish did occur, the impact would likely be greatest initially following introduction. Restoration and management efforts for native fish communities should consider the presence of invasive species, such as flathead catfish, in coastal Atlantic slope rivers. The presence of a voracious predator such as flathead catfish could hamper the success of these efforts via direct predation of species of interest to managers.

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Table 1. Frequent representatives from each diet group found in flathead catfish stomachs in Contentena Creek, Northeast Cape Fear River, and the Lumber River, 2001-2002.

Group	Common names of typical representatives
Baetidae	Mayflies
Cambaridae	Crayfish
Catostomidae	Suckers
Centrarchidae	Sunfish, i.e. bluegill, red breast, and largemouth bass
Clupeidae	Hickory shad
Corbiculadae	Asian clam
Corydalidae	Hellgrammites
Cyprinidae	Coastal shiners, eastern silvery minnows, and others
Ictaluridae	Catfish, i.e. channel, blue, and flathead catfish
Odontidae	Dragonflies
Penaidae	White shrimp
Percidae	Darters, yellow perch
Soleidae	Hogchokers
Trichoptera	Caddisflies
Unknown Invertebrates	Insect wings, carapace pieces
Unknown Fish	Fish flesh, backbone, scales

Table 2. Year, river, prey item, frequency of occurrence, and rank of stomach items. Zero values indicate a group that was not identified in the stomach contents for that year and river.

2001

	Contentnea Creek		Northeast Cape Fear River		Lumber River	
Group	Percent	Rank	Percent	Rank	Percent	Rank
Baetidae	0.0		10.3	5	0.0	
Cambaridae	26.3	2	27.6	2	28.6	2
Catostomidae	2.5	9	0.0		0.0	
Centrarchidae	18.8	3	20.7	3	28.6	2
Clupeidae	3.8	6	0.0		0.0	
Corbiculadae	2.5	9	0.0		0.0	
Corydalidae	3.8	6	0.0		0.0	
Cyprinidae	7.5	4	0.0		0.0	
Ictaluridae	1.3	11	6.9	6	0.0	
Odontidae	0.0		3.5		0.0	
Penaidae	7.5	4	0.0		0.0	
Percidae	3.8	6	0.0		0.0	
Soleidae	2.5	9	17.2	4	0.0	
Trichoptera	0.0		3.5	7	0.0	
Unknown Invertebrates	1.3	11	3.5	7	0.0	
Unnknown Fish	57.5	1	55.2	1	57.1	1
Number of flathead catfish stomachs:						
with contents	80		29		7	
empty	96		71		16	

Table 2 continued.

2002

Group	Contentnea Creek Percent	Contentnea Creek Rank	Northeast Cape Fear River Percent	Northeast Cape Fear River Rank	Lumber River Percent	Lumber River Rank
Baetidae	1.2	8	0.0		6.7	6
Cambaridae	27.4	2	60.3	1	33.3	2
Catostomidae	2.4	7	0.0		0.0	
Centrarchidae	14.3	4	6.9	5	13.3	3
Clupeidae	0.0		0.0		0.0	
Corbiculadae	0.0		1.7	6	0.0	
Corydalidae	1.2	8	0.0		0.0	
Cyprinidae	1.2	8	0.0		0.0	
Ictaluridae	6.0	5	1.7	6	13.3	3
Odontidae	1.2		0.0		0.0	
Penaidae	6.0	5	0.0		0.0	
Percidae	15.5	3	0.0		13.3	3
Soleidae	2.4	7	8.6	3	0.0	
Trichoptera	0.0		0.0		0.0	
Unknown Invertebrates	1.2	8	8.6	3	6.7	6
Unnknown Fish	62.0	1	32.8	2	60.0	1
Number of flathead catfish stomachs:						
with contents	84		58		15	
empty	70		57		9	

Table 3. Year, river, prey group, mean percent frequency of that group, standard error and rank of stomach groups found in flathead catfish. Zero values indicate a group that was not identified in the stomach contents in that river or year.

2002

	Contentnea Creek			Northeast Cape Fear River			Lumber River		
Group	Mean %	SE	Rank	Mean %	SE	Rank	Mean %	SE	Rank
Baetidae	0.0	0.0		5.9	0.0	6	0.0	0.0	
Cambaridae	18.7	4.1	2	24.1	7.7	2	26.8	18.4	2
Catostomidae	1.7	1.3	8	0.0	0.0		0.0	0.0	
Centrarchidae	9.5	2.6	3	9.0	4.2	4	23.8	15.8	3
Clupeidae	0.9	1.8	5	0.0	0.0		0.0	0.0	
Corbiculadae	1.3	0.9	10	0.0	0.0		0.0	0.0	
Corydalidae	2.2	1.4	5	0.0	0.0		0.0	0.0	
Cyprinidae	5.5	2.4	4	0.0	0.0		0.0	0.0	
Ictaluridae	1.3	1.3	10	6.9	4.8	5	0.0	0.0	
Odontidae	0.0	0.0		1.2	1.2	8	0.0	0.0	
Penaidae	2.8	1.4	6	0.0	0.0		0.0	0.0	
Percidae	2.8	1.7	6	0.0	0.0		0.0	0.0	
Soleidae	1.7	1.3	8	11.7	5.3	3	0.0	0.0	
Trichoptera	0.0	0.0		1.7	1.7	7	0.0	0.0	
Unknown Invertebrate	0.6	0.6	12	0.7	0.7	9	0.0	0.0	
Unknown Fish	49.0	5.1	1	38.8	7.5	1	47.6	0.0	1
Number of flathead catfish stomachs:									
with contents	80			29			` 7		
empty	176			100			23		

Table 3 continued.

	2002								
	Contentnea Creek			Northeast Cape Fear River			Lumber River		
Group	Mean %	SE	Rank	Mean %	SE	Rank	Mean %	SE	Rank
Baetidae	0.3	0.2	13	0.0	0.0		1.7	1.7	7
Cambaridae	19.3	3.9	2	53.4	6.1	1	42.8	9.9	1
Catostomidae	2.5	1.7	7	0.0	0.0		0.0	0.0	
Centrarchidae	7.0	2.3	4	4.8	2.7	4	5.1	3.5	3
Clupeidae	0.0	0.0		0.0	0.0		0.0	0.0	
Corbiculadae	0.0	0.0		0.4	0.4	7	0.0	0.0	
Corydalidae	0.6	0.6	11	0.0	0.0		0.0	0.0	
Cyprinidae	1.2	1.2	8	0.0	0.0		0.0	0.0	
Ictaluridae	3.4	1.8	5	0.9	0.9	6	3.3	3.3	5
Odontidae	0.4	0.4	12	0.0	0.0		0.0	0.0	
Penaidae	3.1	1.5	6	0.0	0.0		0.0	0.0	
Percidae	9.1	2.8	3	0.0	0.0		4.3	3.4	4
Soleidae	0.7	0.6	10	4.6	2.2	5	0.0	0.0	
Trichoptera	0.0	0.0		0.0	0.0		0.0	0.0	
Unknown Invertebrate	1.2	1.2	8	7.5	3.3	3	1.9	1.9	6
Unknown Fish	51.5	4.9	1	28.5	5.7	2	38.7	10.1	2
Number of flathead catfish stomachs:									
with contents	84			58			15		
empty	74			57			9		

Table 4. Year, river, prey group, total weight (g) of group in stomach contents, percentage of the total weight for all stomach contents, and rank (ascending order) of stomach items found in flathead catfish. Zero values indicate a group that was not identified in the stomach contents in that river or year.

	2001								
	Contentnea Creek			Northeast Cape Fear River			Lumber River		
Group	Total weight	%	Rank	Total weight	%	Rank	Total weight	%	Rank
Baetidae	0.0	0.0		0.04	0.03	6	0.0	0.0	
Cambaridae	23.6	4.0	4	34.3	27.7	2	0.5	12.1	3
Catostomidae	5.8	1.0	7	56.9	0.0		0.0	0.0	
Centrarchidae	286.1	48.2	1	13.4	45.9	1	2.0	51.8	1
Clupeidae	16.7	2.8	5	0.0	0.0		0.0	0.0	
Corbiculadae	0.8	0.1	10	0.0	0.0		0.0	0.0	
Corydalidae	0.9	0.1	10	0.0	0.0		0.0	0.0	
Cyprinidae	2.4	0.4	9	0.0	0.0		0.0	0.0	
Ictaluridae	5.1	0.9	8	13.4	10.9	5	0.0	0.0	
Odontidae	0.0	0.0		0.3	0.02	7	0.0	0.0	
Penaidae	0.4	0.1	12	0.0	0.0		0.0	0.0	
Percidae	170.9	28.8	2	0.0	0.0		0.0	0.0	
Soleidae	6.8	1.2	6	6.8	5.5	5	0.0	0.0	
Trichoptera	0.0	0.0		0.0	0.0		0.0	0.0	
Unknown Invertebrate	0.01	0.0		0.01	0.01	8	0.0	0.0	
Unknown Fish	74.0	12.5	3	12.4	10.0	4	1.4	36.1	2
All fish total		95.7			72.3			87.9	
All invertebrate total		4.3			27.8			12.1	
Number of flathead catfish stomachs:									
with contents	80			29			` 7		
empty	96			71			16		

Table 4 continued.

	2002								
	Contentnea Creek			Northeast Cape Fear River			Lumber River		
Group	Total weight	%	Rank	Total weight	%	Rank	Total weight	%	Rank
Baetidae	0.02	0.1	11	0.0	0.0		0.01	0.1	7
Cambaridae	38.1	10.1	3	114.2	52.4	1	18.5	14.6	4
Catostomidae	13.7	3.6	4	0.0	0.0		0.0	0.0	
Centrarchidae	245.9	65.0	1	40.4	18.5	3	27.4	21.7	2
Clupeidae	0.0	0.0		0.0	0.0		0.0	0.0	
Corbiculadae	0.0	0.0		5.2	2.4		0.0	0.0	
Corydalidae	0.2	0.0	11	0.0	0.0		0.0	0.0	
Cyprinidae	1.3	0.3	8	0.0	0.0		0.0	0.0	
Ictaluridae	8.8	2.3	6	6.6	0.0		55.8	44.1	1
Odontidae	0.2	0.1	12	0.0	3.0	4	0.0	0.0	
Penaidae	1.0	0.3	9	0.0	0.0		0.0	0.0	
Percidae	12.8	3.4	5	0.0	0.0		0.5	0.4	5
Soleidae	2.5	0.7	7	3.5	1.6	6	0.0	0.0	
Trichoptera	0.0	0.0		0.0	0.0		0.0	0.0	
Unknown Invertebrate	0.8	0.2	10	1.2	0.5	7	0.2	0.1	6
Unknown Fish	53.4	14.1	2	46.9	21.5	2	24.1	19.1	3
All fish total		89.3			44.7			85.3	
All invertebrate total		10.7			55.3			14.8	
Number of flathead catfish stomachs:									
with contents	84			58			` 15		
empty	74			57			9		

Table 5. Year, river, prey group, number of identifiable prey from that group, mean weight of identifiable items, standard error of the mean, and rank (ascending order) of stomach items found in flathead catfish. Zero values indicate a group that was not identified in the stomach contents.

	2001											
	Contentnea Creek				Northeast Cape Fear River				Lumber River			
Group	N	Mean	SE	Rank	N	Mean	SE	Rank	N	Mean	SE	Rank
Baetidae	0	0.0	0.0		3	0.01	0.01	6	0	0.0	0.0	
Cambaridae	27	0.8	0.2	8	8	4.3	2.5	3	2	0.2	0.2	3
Catostomidae	2	2.9	2.1	6	0	0.0	0.0		0	0.0	0.0	
Centrarchidae	20	14.3	6.7	2	6	9.5	6.6	1	3	0.7	0.2	1
Clupeidae	3	5.6	3.2	3	0	0.0	0.0		0	0.0	0.0	
Corbiculadae	2	0.4	0.1	9	0	0.0	0.0		0	0.0	0.0	
Corydalidae	3	0.3	0.1	10	0	0.0	0.0		0	0.0	0.0	
Cyprinidae	10	0.2	0.1	11	0	0.0	0.0		0	0.0	0.0	
Ictaluridae	1	5.1	0.0	4	2	6.7	4.6	2	0	0.0	0.0	
Odontidae	0	0.0	0.0		3	0.01	0.0		0	0.0	0.0	
Penaidae	6	0.1	0.03	12	0	0.0	0.0		0	0.0	0.0	
Percidae	6	28.5	27.9	1	0	0.0	0.0		0	0.0	0.0	
Soleidae	2	3.4	3.0	5	6	1.1	0.5	4	0	0.0	0.0	
Trichoptera	0	0.0	0.0		0	0.0	0.0		0	0.0	0.0	
Unknown Invertebrate	1	0.1	0.0	13	1	0.01	0.0	6	0	0.0	0.0	
Unknown Fish	69	1.1	0.8	7	27	0.5	0.1	5	4	0.4	0.1	2
Number of flathead catfish stomachs:												
with contents	80				29				7			
empty	96				71				16			

Table 5 Continued.

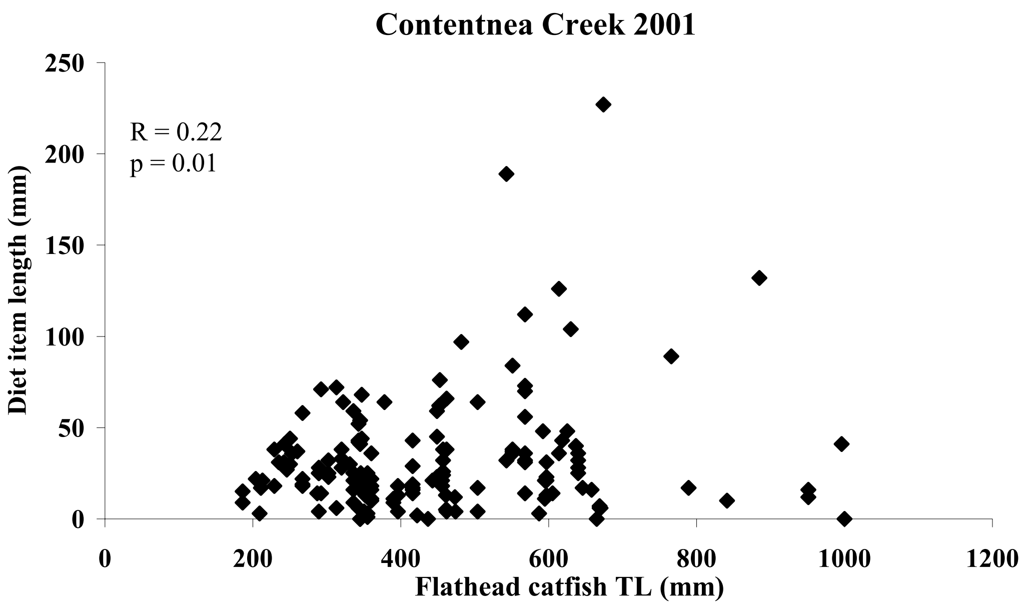
	2002											
	Contentnea Creek				Northeast Cape Fear River				Lumber River			
Group	N	Mean	SE	Rank	N	Mean	SE	Rank	N	Mean	SE	Rank
Baetidae	1	0.02	.	11	0	0.0	0.0		1	0.01	.	7
Cambaridae	30	1.3	0.3	4	43	2.7	0.4	3	16	1.2	0.2	4
Catostomidae	4	3.4	1.7	2	0	0.0	0.0		0	0.0	0.0	
Centrarchidae	17	14.5	7.3	1	5	8.1	3.8	1	4	6.9	0.2	2
Clupeidae	0	0.0	0.0		0	0.0	0.0		0	0.0	0.0	
Corbiculadae	0	0.0	0.0		2	2.6	0.0	4	0	0.0	0.0	
Corydalidae	1	0.2	.		0	0.0	0.0		0	0.0	0.0	
Cyprinidae	1	1.3	.	4	0	0.0	0.0		0	0.0	0.0	
Ictaluridae	5	1.8	0.7	3	1	6.6	.	2	2	27.9	27.9	1
Odontidae	1	0.2	.	10	0	0.0	0.0		0	0.0	0.0	
Penaidae	5	0.2	0.03	10	0	0.0	0.0		0	0.0	0.0	
Percidae	42	0.3	0.03	9	0	0.0	0.0		4	0.1	0.04	5
Soleidae	2	1.2	0.9	6	5	0.7	0.5	6	0	0.0	0.0	
Trichoptera	0	0.0	0.0	0	0	0.0	0.0		0	0.0	0.0	
Unknown Invertebrate	1	0.8	.	7	5	0.2	0.2	7	2	0.1	0.0	6
Unknown Fish	110	0.5	0.2	8	24	2.0	0.1	5	15	1.6	1.2	3
Number of flathead catfish stomachs:												
with contents	84				58				15			
empty	74				57				9			

Table 6. Sample year, sample month, river, sample size, TL (mm) ± SE, Weight (g) ± SE, and stomach fullness ± SE of flathead catfish with stomach contents.

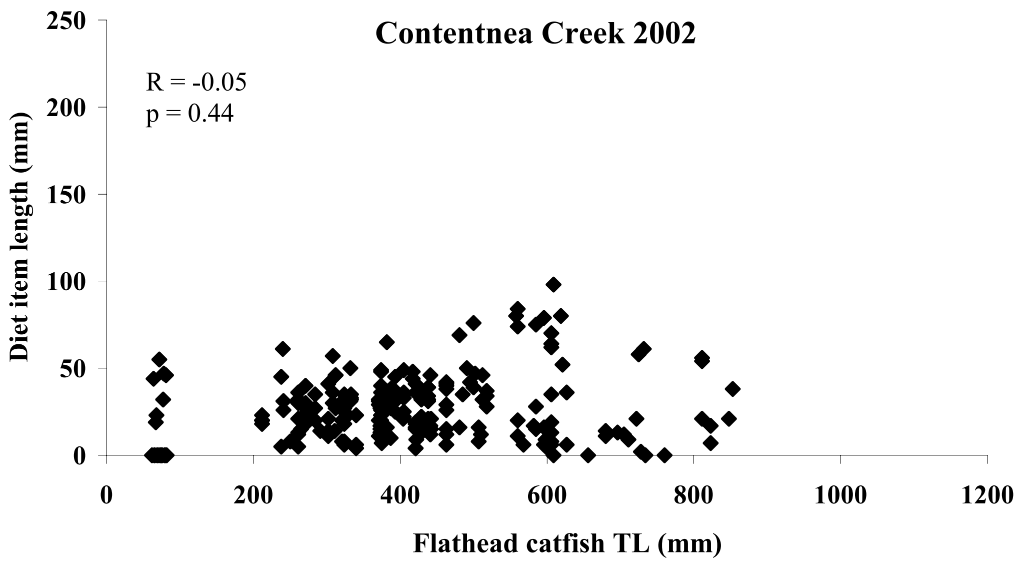
Year	Month	River	N	TL (mm) ± SE	Wt (g) ± SE	Fullness ± SE
2001	July	Contentnea	15	492 ± 45	1,827 ± 432	0.67 ± 0.33
	August	Contentnea	53	455 ± 25	1,636 ± 305	0.33 ± 0.08
	September	Contentnea	13	428 ± 61	1,785 ± 960	0.73 ± 0.35
2002	May	Contentnea	19	498 ± 27	1,688 ± 295	0.20 ± 0.05
	June	Contentnea	23	512 ± 38	2,164 ± 446	0.44 ± 0.17
	July	Contentnea	24	438 ± 35	1,390 ± 366	0.27 ± 0.60
	August	Contentnea	11	301 ± 72	1,504 ± 621	0.30 ± 0.09
2001	July	Lumber	2	572 ± 291	4,225 ± 4025	0.42 ± 0.40
	August	Lumber	2	563 ± 117	2,225 ± 1275	0.95 ± 0.72
2002	April	Lumber	9	654 ± 50	3,823 ± 882	0.27 ± 0.15
	May	Lumber	5	493 ± 67	1,552 ± 452	2.20 ± 1.60
	June	Lumber	1	867 ± 0	7,550 ± 0	0.001 ± 0
	July	Lumber	0			
	August	Lumber	1	447 ± 0	910 ± 0	0.95 ± 0
2001	July	NE Cape Fear	10	407 ± 53	1,205 ± 547	2.40 ± 0.76
	August	NE Cape Fear	12	409 ± 46	1,237 ± 476	3.00 ± 1.32
	September	NE Cape Fear	2	413 ± 139	1,083 ± 867	3.70 ± 3.1
	October	NE Cape Fear	5	420 ± 76	1,029 ± 647	0.47 ± 0.4
2002	April	NE Cape Fear	8	555 ± 88	4,681 ± 3344	1.50 ± 0.53
	May	NE Cape Fear	15	381 ± 46	1,096 ± 390	3.80 ± 1.4
	June	NE Cape Fear	9	298 ± 40	444 ± 265	1.50 ± 1.0
	July	NE Cape Fear	5	449 ± 58	1,216 ± 473	0.28 ± 0.1
	August	NE Cape Fear	19	379 ± 40	989 ± 295	0.41 ± 0.13
	September	NE Cape Fear	5	239 ± 79	1,043 ± 88	0.18 ± 5

Figure Caption

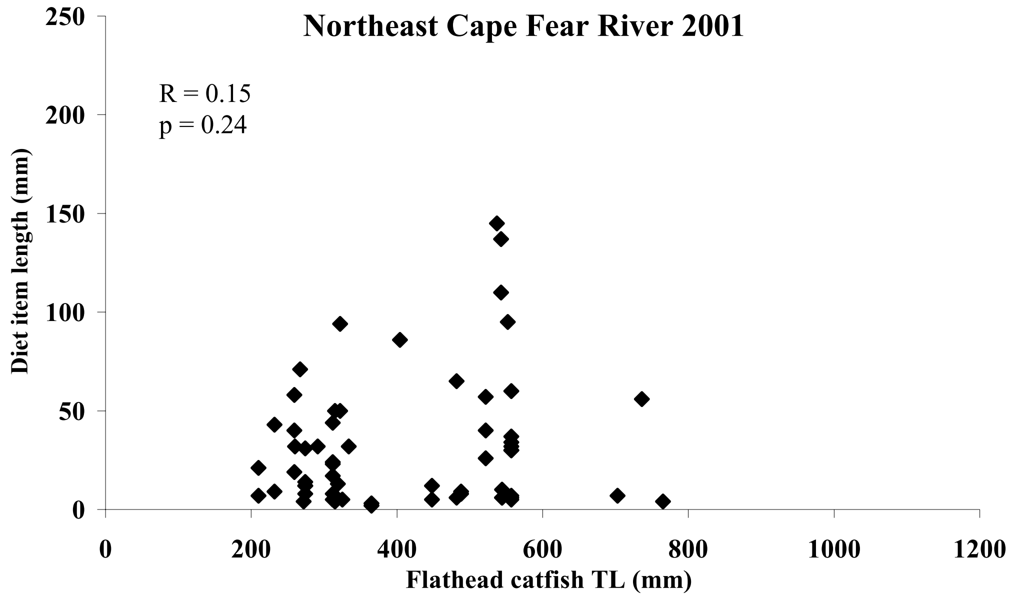
Figure 1. Correlation between diet item size (mm) and flathead catfish (FHC) total length (mm) for Contentnea Creek and the Northeast Cape Fear River in 2001 and 2002. Correlation coefficient (R) and p values are shown.



Contentnea Creek 2001
R = 0.22
p = 0.01
Diet item length (mm)
Flathead catfish TL (mm)
0
50
100
150
200
250
0
200
400
600
800
1000
1200



Contentnea Creek 2002
R = -0.05
p = 0.44
Diet item length (mm)
Flathead catfish TL (mm)
0
50
100
150
200
250
0
200
400
600
800
1000
1200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p = 0.24
Diet item length (mm)
Flathead catfish TL (mm)
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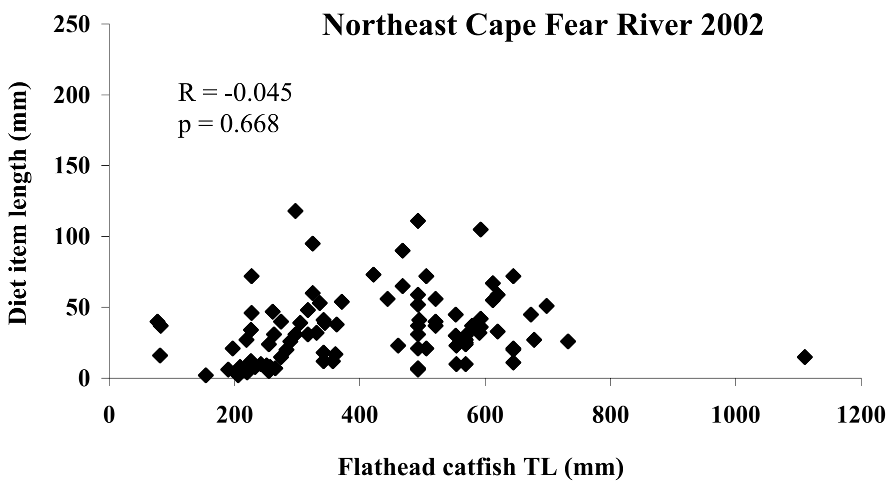
50
100
150
200
250
0
200
400
600
800
1000
1200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Diet item length (mm)
Flathead catfish TL (mm)
0
50
100
150
200
250
0
200
400
600
800
1000
1200

CHAPTER 5

MODELING THE EFFECTS OF AN INTRODUCED APEX PREDATOR ON A COASTAL RIVERINE FISH COMMUNITY

Abstract

The flathead catfish, a carnivorous fish species native to most of the central interior basin of North America, has been introduced into at least 13 U.S. states and one Canadian province. Concurrent declines in abundance of native fishes have been reported in areas where flathead catfish have been introduced. To evaluate the impact of this invasive species on the native fish community, I developed an ecosystem simulation model (including flathead catfish) based on empirical data collected for a North Carolina coastal river. Model results suggest that flathead catfish suppress native fish community biomass by 5-50% through both predatory and competitive interactions. However, these reductions could be mitigated through sustained exploitation of flathead catfish by recreational or commercial fishers at levels equivalent to those for native flathead catfish populations (annual exploitation = 6-25%). These findings demonstrate the potential for using directed harvest of an invasive species to assist in restoring native ecosystems and contribute to the growing global demand for fish products as a human food source.

Introduction

The introduction and establishment of non-native species is a widespread and poorly understood global phenomenon. While most species introductions fail or persist unnoticed (Williamson 1996), some lead to declines in the abundance or diversity of native species– and occasionally cascading negative ecosystem level effects which impact human populations (Folkerts 1997). The annual economic impact of the 50,000 nonnative species that have been introduced into the United States is about U.S. $137 billion (Pimentel et al. 2000)– an amount 13 times larger than the 2003 budget for the Department of Interior, the primary United States governmental agency charged with conservation and management (U.S. Department of the Interior, Office of the Budget Director). This cost does not include the impacts of species that have been translocated within the United States and their potential effect (Pimentel et al. 2000).

Generalizations describing the biotic and abiotic characteristics that regulate the success or failure of an invasive species have been derived based on field, experimental, and theoretical studies (Elton 1958; Williamson 1996), and the resulting body of literature describing invasive species is immense. Invading species encounter environmental (e.g., suitable habitat), biotic (e.g., competition), and demographic (e.g., reproductive traits) resistance that must be overcome to establish a self-sustaining population (Moyle and Light 1996a). Failure in any one of these areas usually leads to the invasion failing (as most do). However, in situations where invasive species have been purposefully introduced for food or recreation, humans have often selected species with desirable (to humans) physical traits (e.g., large size, palatable flesh) and introduced these species repeatedly into ecosystems that are more vulnerable to invasion (e.g., highly disturbed or degraded systems) (Moyle and Light 1996b). This human intervention increases the likelihood of a successful invasion by circumventing many of the naturally existing invasion obstacles.

While often not as captivating as introductions from regions outside of the United States, translocations of nonnative species within the country have had dramatic impacts on aquatic ecosystems. Community compositions in both coastal and inland aquatic ecosystems in the United States have been widely and severely altered by species introductions. For example, two endemic Atlantic slope fishes, striped bass *Morone saxatilis* and American shad *Alosa sapidissima,* were both introduced and established along the United States west coast in the 19^{th} century, and largemouth bass *Micropterus salmoides*, with a native range primarily in the Mississippi River valley and southern Atlantic slope, is now found throughout North America and around the world (Li and Moyle 1993; Nielsen 1993). It is clear that fish faunas across the continental United States are becoming more similar through widespread introductions of fish species intended to enhance food and sport fisheries (Rahel 2000). However the effects of these species introductions are not fully understood and are rarely considered until after the introduced species has become established, greatly limiting management options.

The flathead catfish *Pylodictis olivaris* is a large piscivorous catfish native to most of the interior US throughout the Rio Grande, Mississippi, and Mobile River drainages (Smith-Vaniz 1968; Jenkins and Burkhead 1994). Flathead catfish have been legally and illegally introduced into at least 13 United States (primarily along the Atlantic slope) and one Canadian province (Jackson 1999) usually in an effort to establish recreational fisheries. Within 15 years following their introduction into North Carolina (only documented introduction is of 11 individuals), flathead catfish have expanded to cover a 200-km reach of the Cape Fear River and have emerged as the dominant predator within the drainage basin (Guier et al. 1981).

Flathead catfish are widely prized throughout their native range as a trophy sportfish due to their large size (current world angling record 56.4 kg), fighting ability when hooked, and highly palatable flesh. These qualities support recreational and commercial fisheries throughout their native range and developing fisheries throughout their introduced range (Quinn 1993; Jackson 1999; Travnicheck and Clemmons 1999). Unlike most other catfishes, flathead catfish are obligate carnivores and primarily piscivorous, and given their potential to reach large sizes, their feeding patterns have been widely studied to discern their interactions with other fish species. Swingle (1967) documented that flathead catfish >254-mm total length "may compete with fishermen for fish of harvestable size" in ponds. Results from similar diet studies, as well as widespread concern over declining populations of native fishes following flathead catfish introduction, have compelled study of flathead catfish food habits in their introduced range (Guier et al. 1981; Ashley and Buff 1987; Quinn 1987; Thomas 1995). These studies generally document a decline in native sportfish populations (likely via predation) following introduction of flathead catfish. The species affected are usually native centrarchids and ictalurids, but other natives including the federally endangered razorback sucker *Xyrauchen texanus* in the San Pedro River, Arizona, are thought to be threatened by flathead catfish introduction (Marsh and Brooks 1989).

In this paper, I develop an ecosystem model including flathead catfish in a North Carolina coastal plain river based on empirical data from the system. Given the seemingly ever increasing global demand for fish products, the ability of humans to alter aquatic ecosystems through intensive fishing efforts (Jackson et al. 2001), the popularity of flathead catfish as a food fish in its native range (Jackson 1999), and the large recreational and commercial fisheries interest in North Carolina (National Marine Fisheries Service 2001), flathead catfish may be an excellent candidate species to promote for more intensive harvest. Flathead catfish harvest would provide a desired food product and may also help restore native ecosystems by reducing the biomass of an invasive species. Here I examine how manipulating exploitation rates of flathead catfish affects their abundance and ecological role in structuring the native fish community. These simulations may prove useful in management scenarios for established and newly introduced populations of flathead catfish and for understanding the ecological consequences of this and other introduced species.

Methods

Model Design

I developed an ecosystem simulation model based on Contentnea Creek (35°20'03"N 77°22'73"W), a large tributary of the Neuse River in eastern North Carolina, using an Ecopath and Ecosim framework (Walters et al. 1997; Christianson et al. 2000). The initial model is a static mass balance of the production and losses of the biomass for each component of an ecosystem. Balance is achieved when production and immigration is equal to predatory losses, nonpredatory mortality, harvest, and emigration. Because all variables are linked within a food web, changes in one variable are expressed as changes in other (often many) components of the web. Flow and linkages are established among different components of the food web model. A second model (Ecosim) simulates changes in the initial "balanced" steady-state of the food web (the Ecopath model) with altered exploitation rates, species interactions, environmental changes, or a combination of factors. Similar models have been used to examine the linkages between primary production, fish production, and fishery exploitation in marine and freshwater systems and also the linkage between plant community biomass, herbivore density, and predator density in the Canadian arctic (Krebs et al. 2003). Explicit details of the modeling approach are published elsewhere (Walters et al. 1997; Christianson et al. 2000).

My model was developed incorporating empirical data from a multi-investigator project evaluating the interaction between flathead catfish and native fish communities in North Carolina coastal plain rivers (NCWRC report). Most field sampling efforts occurred during spring through early fall of 2000-2003 when warm water temperatures were conducive to sampling both introduced and native fishes (Chapter 3). My model was composed of 12 functional groups: nine fish, one invertebrate, one plankton, and one detritus (Table 1). Fish were grouped based on similar morphometric, feeding, and life-history functional attributes (Table 1). For example, flathead catfish were placed in an "exotic piscivore" group while all darters (*Percina* and *Etheostoma spp*.) and minnows (*Notropis spp*.) were placed in a single "omnivore-collector" group.

Model initialization required estimates for each functional group of habitat area used, biomass (B), production:biomass ratio (P:B), consumption:biomass ratio (Q:B), diet information, and biomass harvested. As much as possible, this information was derived empirically for each functional group. For example, estimates of instantaneous mortality (Z) were obtained for flathead catfish using catch-curve analysis (NCWRC report), while mortality estimates for other functional groups were calculated by dividing the annual production for each functional group by its biomass. Biomass for each fish functional group was estimated by first calculating the abundance for each individual species using a three-pass removal method (Seber 1982). Individual fish weights were measured in the field, and the average weight was assigned to each species in the functional group. A weighted average (weighted by species abundance) was then used to calculate the mean biomass for that entire functional group. Capture histories from the removals were pooled for each functional group to develop a group-wide capture-probability to allow abundance estimation for the species where removal estimates were not possible (Appendix 1). Contentnea Creek supports spring runs of anadromous shad (*Alosa* spp.) and striped bass, which occurred prior to my sampling. For this modeling effort, I only considered the sizes and densities of each genus collected during my sampling period. Thus, only juvenile *alosids* (a prey item) and resident striped bass (a predator found in low numbers, which does not return to the marine environment in a given year) are included in my model.

Removal population estimates were conducted in late spring and early fall, thus approximate annual P:B ratio values could be calculated by subtracting the biomass of a functional group in the fall from that group's biomass in the spring and dividing by the spring biomass. Q:B ratios for each species were calculated using the online estimator available through Fishbase (www.fishbase.org), which is based on equations provided in Pauly (1986) and Palomares and Pauly (1989). An average Q:B for each functional group was then calculated using a weighted mean (by abundance of each individual species). Diet matrices were developed from empirical diet samples conducted in conjunction with this study (for flathead catfish) or from published reports (Appendix 2).

Exploitation rates for all fish species in Contentnea Creek are relatively low, primarily due to the remote location and limited stream access. Harvest occurs for several species included in my model, primarily native *Lepomis spp., Micropterus spp.*, striped bass, and flathead catfish. I used an estimated annual biomass exploitation level (u) for flathead catfish for modeling efforts of 4% based on harvest rates of a group of fish radio-tagged as part of another aspect of my study (W. E. Pine, unpublished data). Because of uncertainty associated with this exploitation rate, I simulated a wide range of exploitation rates that cover most potential exploitation levels for flathead catfish in this and other systems. Exploitation estimates for other species were derived from the literature. Recreational fisheries for flathead catfish in native rivers are estimated to have annual exploitation rates of 25% or more (Vince Travnichek, Missouri Department of Conservation and Natural Resources, Columbia, Missouri, *personal communication*) and in introduced populations between 14 and 25% (Quinn 1993). Combined with commercial fisheries, total exploitation rates could be higher. All model parameters are provided in Appendix 2.

Model Application and Scenarios

Following the introduction of an invasive species, resource management agencies frequently focus their efforts on eradication options for the invader. However, invasive species may become well established before management actions occur, and complete removal is rarely a viable option. Instead, resource management agencies may become interested in the impacts of the invasive species on native species and how manipulation of invasive species abundance might impact native populations. Because many fish species (including flathead catfish) represent a marketable food product, and fisheries management agencies, commercial fishing interests, and recreational anglers have a history of manipulating and exploiting fish populations, I used this model to evaluate how native fish communities would respond to varying reductions in flathead catfish populations via intensive exploitation. I evaluated three different model scenarios (1) changes in the native fish community under a modeling scenario which emulates the original introduction of flathead catfish in a coastal North Carolina river, (2) evaluation of ecosystem response to high levels of flathead catfish exploitation in an attempt to extirpate flathead catfish from a coastal river, and (3) native fish response to sustained exploitation of flathead catfish across a range of exploitation levels similar to those found for native populations of flathead catfish.

Historical Invasion Analysis

I used historical information on the introduction of flathead catfish in North Carolina to evaluate the predicted response and rate of change by the native fish community to flathead introduction. The only documented release of flathead catfish into North Carolina waters was a single release of 11 individuals with a total weight of 107 kg into the Cape Fear River, a large North Carolina coastal plain river about 75 km southeast of Contentnea Creek (Guier et al. 1981). The source or date of the flathead catfish introduction in Contentnea Creek is not known. As a general assessment of my overall modeling approach, I evaluated how early reports of the rapid growth in the flathead catfish population and subsequent changes within the native fish community compare to the predictions of my model. Because this model is based on an ecosystem that already contains flathead catfish, the invasion scenario was developed differently than the scenarios below. First, flathead catfish exploitation was simulated to be very high, in effect removing flathead catfish from the system. The ecosystem without flathead catfish was then allowed to reach equilibrium. This equilibrium was considered to simulate the ecosystem in the absence of flathead catfish. Flathead catfish were then added to the ecosystem at the same population biomass as the Cape Fear River introduction, and the ecosystem response was measured from this point.

Sustained Fishing Pressure

I simulated the population level responses of the native fish groups to a variety of flathead catfish exploitation levels. The simulated exploitation levels (u) of 6 and 25% cover the range of reported flathead catfish exploitation in native and introduced populations. Each of these exploitation levels were sustained for 10 years. The resiliency of both flathead catfish and native fish populations to increased flathead catfish exploitation was then examined by reducing exploitation to current levels and monitoring ecosystem response.

I then evaluated a "maintenance control" option where flathead catfish exploitation oscillates between a 5-year high exploitation period (u = 25%) and a reduced exploitation period (u = 6%) for 5 years. Again, simulated exploitation levels mimic actual reported rates for native populations of flathead catfish. These reported rates are exclusively from recreational fishing although commercial fishing could also have the same or greater impact.

Flathead Catfish Eradication

Management agencies often consider efforts to remove invasive species to help restore ecosystems to their native condition. I examined ecosystem response to an effort to eliminate flathead catfish by simulating an intensive removal effort via simulated exploitation of 33 and 54% (10 and 20 times current levels) sustained for 10 years. Intensive exploitation was then stopped, and ecosystem response was monitored for 10 years as above. Additionally, long-term resiliency to intensive exploitation was evaluated by conducting the same eradication simulations, but monitoring the ecosystem for longer time periods, 50 years for the u= 33% and 100 years for the u= 54% scenario. These exploitation rates could be achieved through resource agency personnel targeting flathead catfish for removal through scientific sampling in conjunction with commercial and recreational fishing efforts.

Results

Invasion

My invasion simulation was initiated with the same "introduction" biomass as the original flathead catfish release into the Cape Fear River. This simulation resulted in declines of about 30% in the anadromous shad and native insectivore groups and about a 50% decline in the anadromous and native piscivore groups (Figure 1). Other groups declined by about 5-15% with the exception of native detritivores, which increased by about 30% (Figure 1). In this invasion scenario, flathead catfish were predicted to become the dominant apex piscivore by population biomass in less than 50 years.

Sustained Fishing Pressure

Currently exploitation for flathead catfish in Contentnea Creek is low, about 4% per year. My model predicted that reducing flathead catfish biomass via increasing exploitation rates to 6% would lead to only a 2-3% increase in most native fish groups (Figure 2). As exploitation rate increases, flathead catfish biomass declines, and native fish biomass increases. Increases in population biomass of about 25-75% were predicted for native piscivores, native insectivores, anadromous piscivores, and estuarine species in less than 10 years following an increase in flathead catfish exploitation to either 25 or 33% (Figure 2). Other native fish groups including omnivores and omnivore collectors also showed population biomass increases of 2-10%. If higher fishing pressure is not sustained, population biomass of all functional groups are predicted to return to pre-increased fishing levels in less than 10 years.

Eradication Efforts

Simulated flathead catfish exploitation levels of more than 33% were not sustainable, and at this level flathead catfish were nearly eliminated from the system by harvest. At 33% exploitation, flathead catfish biomass was reduced by about 90% within 10 years (Figure 3). A larger increase in exploitation (54% exploitation) reduced flathead catfish biomass by about 95% within 5 years nearly extirpating flathead catfish from the system for at least 15 years. This reduction in flathead catfish biomass resulted in the biomass doubling for native and anadromous piscivores, an approximate 50% increase for native insectivores, anadromous shad, and estuarine species, and biomass increases of 5-15% for native omnivores and omnivore-collectors.

Resiliency to Exploitation

My simulations demonstrate flathead catfish resiliency to exploitation. If exploitation ranges from 6 - 33% for a period of 10 years and then is reduced to current levels (about 4%), flathead catfish populations will return to their initial biomass within 5-50 years, and subsequently reduce native fish populations to pre-exploitation levels (Figures 2, 4). Under a modeling scenario of very high exploitation levels (54% exploitation) sustained for 10 years flathead catfish populations were predicted to crash (0.01% of original biomass), yet recover from this intense harvest and return to original levels in about 80 years (Figure 4).

The maintenance control management scenario (alternating 5-year periods of high and low exploitation) dampened the observed resiliency to decreased fishing pressure and maintained relatively high positive increases in native fish biomass (Figure 5). As previously predicted, the greatest change in native fish abundance came when flathead catfish abundance was lowest (u = 25%). However, even when fishing pressure was reduced (u =6%) following five years of high fishing pressure, biomass of most native fish was still much higher than it would have been at the low fishing rate alone. Average biomass response during the maintenance control simulations for recreationally important species was highest for native and anadromous piscivores (approximately 70% increase each), followed by native insectivores and anadromous shad (approximately 30% increase each). Average flathead catfish biomass reductions were approximately 70%.

Discussion

The results of this modeling exercise suggest that reduction of flathead catfish biomass via exploitation may allow an increase in population biomass of a variety of native fish groups. Native apex predators in my model (native and anadromous piscivore groups) showed the greatest response to the initial introduction and reductions in flathead catfish populations, likely because of interspecific competition with flathead catfish for available food resources. Native insectivores also showed strong positive increases in biomass following increased exploitation. Native omnivores and the omnivore-collector group were both predicted to increase following reductions in flathead biomass. Although neither of these groups competes directly with adult flathead catfish for food resources, they are both comprised of flathead catfish prey items– thus reduction in flathead catfish biomass reduces total mortality of these groups, increasing biomass. The native-omnivore collector group is comprised of native darter and minnow species, groups that are particularly sensitive to anthropogenic changes in aquatic environments. The additional survival pressure on these groups induced by an invasive predator species could be particularly detrimental in an already stressed physical environment.

Two groups showed unexpected results associated with declines in flathead catfish biomass. The estuarine group was composed primarily of hogchokers *Trinctes maculatus*, and the unique body shape of this benthic flatfish was easily identified in the flathead catfish diet samples. This may have led to an over-representation of hogchokers in the model diet matrix for flathead catfish, and coupled with their natural low biomass in the system, their response to reductions in flathead catfish biomass may be exaggerated.

Native detritivores generally declined in biomass as exploitation rates increased for flathead catfish. The mechanism for these declines may be greater predation mortality on this group from the native and anadromous piscivore groups that were released from competition with flathead catfish. My native detritivores group included several redhorse (*Moxostoma* spp.) species, a group which corollary declines in abundance have been found in areas where flathead catfish have been introduced (Bart et al. 1994). Conversely, Guier et al. (1981) observed an increase in percent occurrence of *Moxostoma sp*. in the Cape Fear River following flathead catfish introduction, similar to the results of my modeling for the native detritivore group. These conflicting findings are not unexpected given the varying impacts invasive species can have on different ecosystems (Chapter 6). This model was developed for a very similar system as Guier et al. (1981) thus similarity between the model predictions and empirical observations are expected. An Ecopath model for the systems examined by Bart et al. (1984) may be similar to those systems.

Restoration efforts for anadromous shad are currently underway in several rivers along the Atlantic slope of the United States (Beasley and Hightower 2000). My model included a juvenile anadromous shad component from my summer sampling of these fish before they outmigrated to the ocean. The predicted increase in biomass for anadromous shad as flathead catfish exploitation increased is particularly important to these restoration efforts. In many fish species growth and survival during early life can affect adult fish abundance (Houde 1987). Decreasing mortality at early life stages (such as the juveniles) can potentially have large impacts on adult abundance. Resource managers should consider increased juvenile and adult predation mortality from invasive predators such as flathead catfish in designing restoration programs for anadromous shad species across the Atlantic slope.

Complete elimination of flathead catfish is likely difficult from Contentnea Creek or any coastal river where flathead catfish have become established. I documented flathead catfish migration from Contentnea Creek throughout most of the Neuse River (NCWRC Final Report). Because of this movement, the flathead catfish population is continuous throughout the Neuse River basin instead of smaller discrete population units making erradication options unrealistic. Aquatic plant managers are accustomed to dealing with similar issues in designing control options for invasive aquatic plant species where efforts are directed at maintaining the population of the invasive species at the lowest feasible levels rather than complete eradication (Pieterse and Murphy 1990). By using maintenance control techniques to keep populations at low densities, less time and financial resources are actually expended by continuously harvesting populations, rather than by allowing population to expand to large levels, and then attempting to reduce them. My maintenance control simulations clearly demonstrate that this approach is possible with invasive flathead catfish. In fact, the average population response for each native species group in the maintenance control scenario (Figure 3) was at least twice as large as it would be from sustained harvest at the "low" level (6%) (Figure 2).

Apex predators are often the most successful invasive species (Moyle and Light 1996 a, b). This conclusion is based on theory and observations that prey species are usually highly vulnerable to the predation style of the newly introduced predator (Moyle and Light 1996 a). In my model, the groups most strongly affected by changes in flathead catfish biomass are not species that are likely to be heavily preyed upon by flathead catfish (native and anadromous piscivores), but instead are groups competing with flathead catfish for available prey resources (primarily native insectivores). Coastal plain rivers in North Carolina are anthropogenically disturbed (Benniger and Wells 1993; Glasgow and Burkholder 2000) and relatively unproductive with low biomass of native fish species. Because of this low productivity in a disturbed environment, competition for already limited available prey resources with an introduced predator dampens native and anadromous piscivore abundance.

The resiliency of flathead catfish populations to fishing pressure is largely a function of the absence of any natural predator of this species. While several native piscivores in Contentnea Creek are also found in the native range of flathead catfish, and these native predators likely feed on juvenile flathead catfish, this predation pressure is not intensive enough to suppress flathead catfish populations. This is similar to the cane toad *Bufo marinus* invasion in Australia where population densities of cane toads are often much higher in Australia than in the native South American habitats (Lamp and De Leao 1998). This difference in population density between the two continents is primarily a function of higher adult survival in Australia due to a lack of cane toad predators, pathogens, and parasites.

Moyle and Light (1996a) concluded that among environmental, biotic, and demographic factors determining invasion success, environmental factors were the most important, yet overall invasion success depends on the interaction of all three. Contentnea Creek and the larger Neuse River watershed have been broadly affected by anthropogenic and natural disturbance including flow regime alterations, poor land use practices, nutrient enrichment and hurricanes (Cahoon et al. 1999; Paerl et al. 2001). All of these factors may combine to lessen the invasion resistance of the native fish community. From an ecologically detrimental invasive species perspective, flathead catfish represent the ideal aquatic invader due to its predatory nature, broad habitat use (small and large lentic and lotic systems), and appealing sporting characteristics to human users who have fostered their introduction into new areas. However, while these traits may lend the species to successful introducton and establishment in a wide variety of systems, they make the management of this invasive species much more difficult.

Management Implications

My modeling results have shown that moderate, sustained levels of flathead catfish exploitation may release native fish groups from predation by and competition with flathead catfish. This finding is important for resource managers involved in restoring native fish populations in areas where flathead catfish have been introduced. Management agencies could promote harvest of flathead catfish populations by offering a bounty or subsidy system to commercial fishers in an effort to establish an interest in harvesting this species (by guaranteeing an attractive price) and simultaneously developing a market for the fish product. Increasing the size and intensity of the recreational fishery is an equally important aspect of any effort to reduce flathead catfish biomass and provide sustained fishing pressure. Schramm et al. (1999) found that Mississippi catfish anglers preferred to fish in rivers and streams and that anglers found it very important to “keep a lot of fish” leading those authors to note that “…increased fishing effort and high harvest could deplete these [catfish] resources.”

I found that flathead catfish exploitation rates in native systems (25%) would be more than adequate to provide a large (>30%) increase in most native fish groups. However, this level of exploitation would not likely be sustainable in the rivers I studied, leading to overexploitation of the flathead catfish population—and subsequent declines in catch rates and subsequently a loss of participants in the fishery. Given the resiliency of flathead catfish populations to exploitation, the predicted benefits to native fish groups are only achievable if flathead catfish fishing pressure is sustained to some degree. Declines in exploitation would allow flathead catfish populations to rebound, subsequently losing the gains realized in the native fish communities while flathead catfish populations were suppressed.

Although my simulations suggest that reducing flathead catfish biomass by increasing exploitation rate could release most native fish groups from competition and predation pressures leading to increases in biomass, there are several issues that should be considered in evaluating these results. I examined changes in population biomass of a variety of fish groups in response to exploitation of flathead catfish, which resulted in subsequent changes in other components of the ecosystem through changes in predation mortality or resource competition with other groups. However, size structure of individuals within each of these groups is also likely to change, not just population biomass. For example, flathead catfish exploitation may reduce the number of large individuals in the population, restructuring the population to be dominated by smaller individuals. These smaller individuals may have greater physiological energetic demands than the larger individuals that were removed from the population. Increasing abundance of smaller flathead catfish could result in equal or greater predation pressure on the native fish groups by the exploited flathead catfish population, than by the unexploited population.

My modeling efforts also assume constant recruitment of all fish species. Allen and Pine (2000) showed that changes in population biomass from altering exploitation rates could be masked by variable recruitment in 3 or 5-year study periods for largemouth bass and white crappie *Pomoxis annularis*. Recruitment variability is common in nearly all fish species, thus changes in biomass for any species may be expedited (in years following low recruitment) or delayed (in years following high recruitment). My manipulation of flathead catfish biomass by altering mortality rates also alters total mortality of all other species in the food web by changing predation mortality and competition. Thus, variable recruitment could change the rate at which various components of the ecosystem respond to flathead catfish exploitation.

My model was developed from information collected from an ecosystem that may have already been altered by the invasion of flathead catfish. The current fish assemblage in Contentnea Creek may suffer from the "ghost of predation past" (i.e., the ecosystem impact resulting from predation pressure that occurred in the past remains evident today) such that any potential impact to native species by the exotic was likely prior to this study. It is possible that flathead catfish have extirpated species from Contentnea Creek or reduced population levels below detectable levels. These species would obviously not be included in my model and the interaction between species which no longer exist and other components of the ecosystem cannot be evaluated. My model is based on the current conditions within the ecosystem including impacts of flathead catfish. By manipulating flathead catfish biomass and examining the population release in the native community based on current conditions, I am not basing my predictions on uncertain estimates of past conditions.

Modeling exercises and empirical data both include error and many models may be unreliable for quantitative predictions (Johnson 1995). Models such as the one used here are useful for examining trends in ecosystem dynamics and providing insight into the cascading effects of an invasive species on coastal riverine ecosystems. Given the impossibility of controlled, replicated field studies involving invasive species a modeling method such as this is ecologically the safest approach to elucidate species interactions.

My simulation results suggesting positive responses in native fish biomass following flathead catfish harvest could be considered as a part of a broader ecosystem restoration effort to mitigate the variety of anthropogenic ecosystem alterations in coastal rivers. While many aspects of aquatic ecosystem restoration remain in an experimental phase (Lenihan et al. 1999), our ability to harvest fish populations is well established, and directed harvest toward flathead catfish may represent a conceptually simple, but important step in helping restore native ecosystems.

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Table 1. Species composition of each functional group included in the Ecopath model

Functional Grouping	Species Name
Exotic Piscivore	*Pylodictis olivaris*, Flathead catfish
Native Piscivore	*Pomoxis nigromaculatus*, Black crappie *Amia calva*, Bowfin *Esox niger*, Chain pickerel *Esox americanus*, Redfin pickerel *Micropterus salmoides*, Largemouth bass *Lepisosteus osseus*, Longnose gar
Native Omnivore	*Ictalurus punctatus*, Channel catfish *Erimyzon oblongus*, Creek chubsucker
Native Omnivore-collector	*Umbra pygmaea*, Eastern mudminnow *Hybognathus regius*, Eastern silvery minnow *Aphredoderus sayanus*, Pirate perch *Cyprinella analostana*, Satinfin shiner *Notropis procne*, Swallowtail shiner *Notropis amoenus*, Comely shiner *Etheostoma serrifer*, Sawcheek darter *Percina peltata*, Shield darter *Etheostoma olmstedi*, Tessellated darter *Etheostoma vitreum*, Glassy darter
Native Insectivore	*Lepomis macrochirus*, Bluegill *Lepomis gibbosus*, Pumpkinseed *Lepomis microlophus*, Redear sunfish *Lepomis auritus*, Redbreast sunfish *Gambusia holbrooki*, Eastern mosquitofish
Native Detritivore	*Dorosoma cepedianum*, Gizzard shad *Moxostoma macrolepidotus*, Shorthead redhorse *Moxostoma anisurum*, Silver redhorse
Anadromous Piscivore	*Morone saxatilis*, Striped bass
Estuarine	*Trinectes maculatus*, Hogchoker
Invertebrates	Cambaridae, Crayfish Baetidae, Mayfly
Plankton	
Detritus	

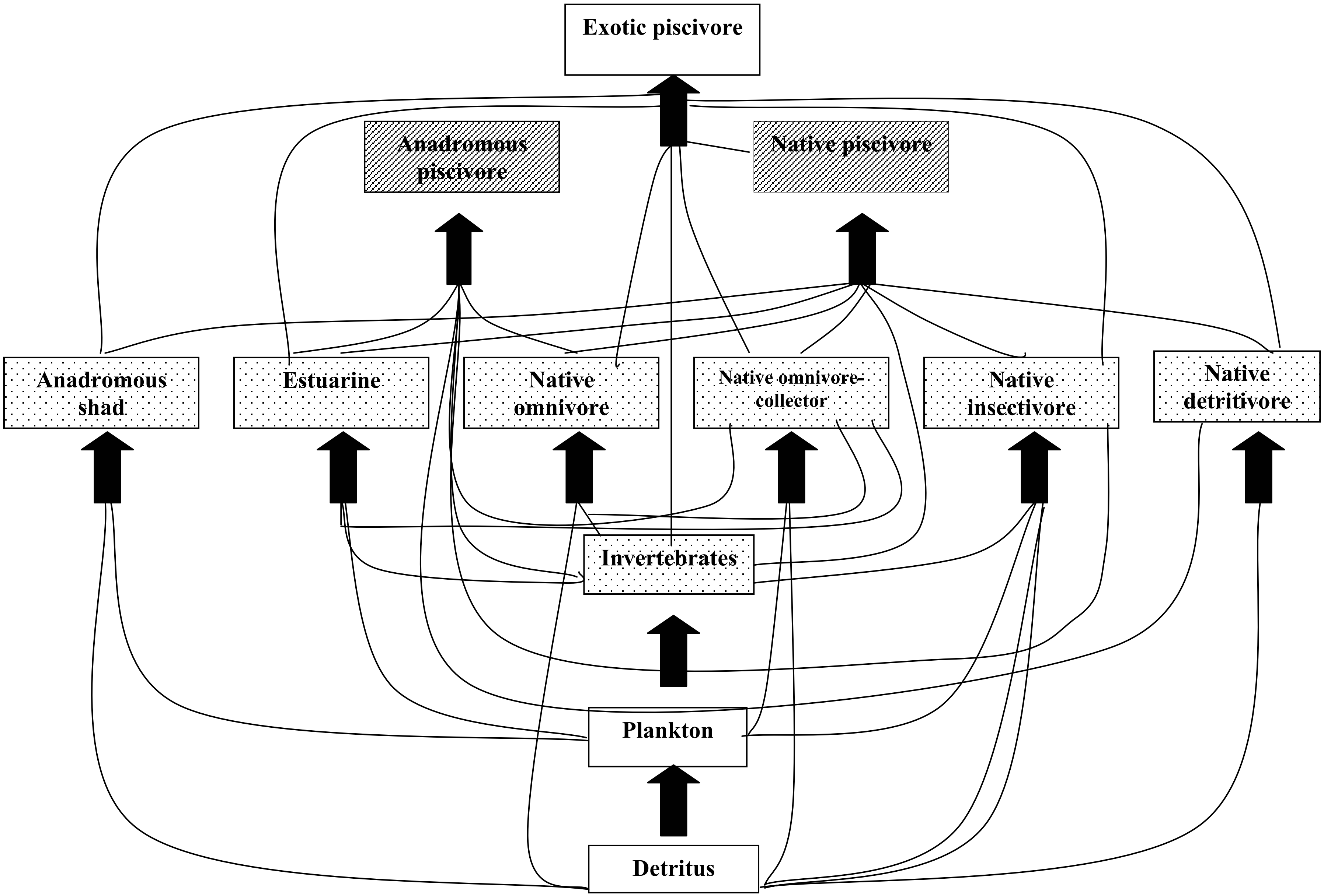


Figure 1. Simplified food web schematic demonstrating linkages among functional groups in Contentnea Creek. Vertical position of each box indicates approximate trophic level. Diagonally shaded boxes represent functional groups which primarily compete with flathead catfish for available food resources, and boxes shaded by dots represent groups consumed by flathead catfish.

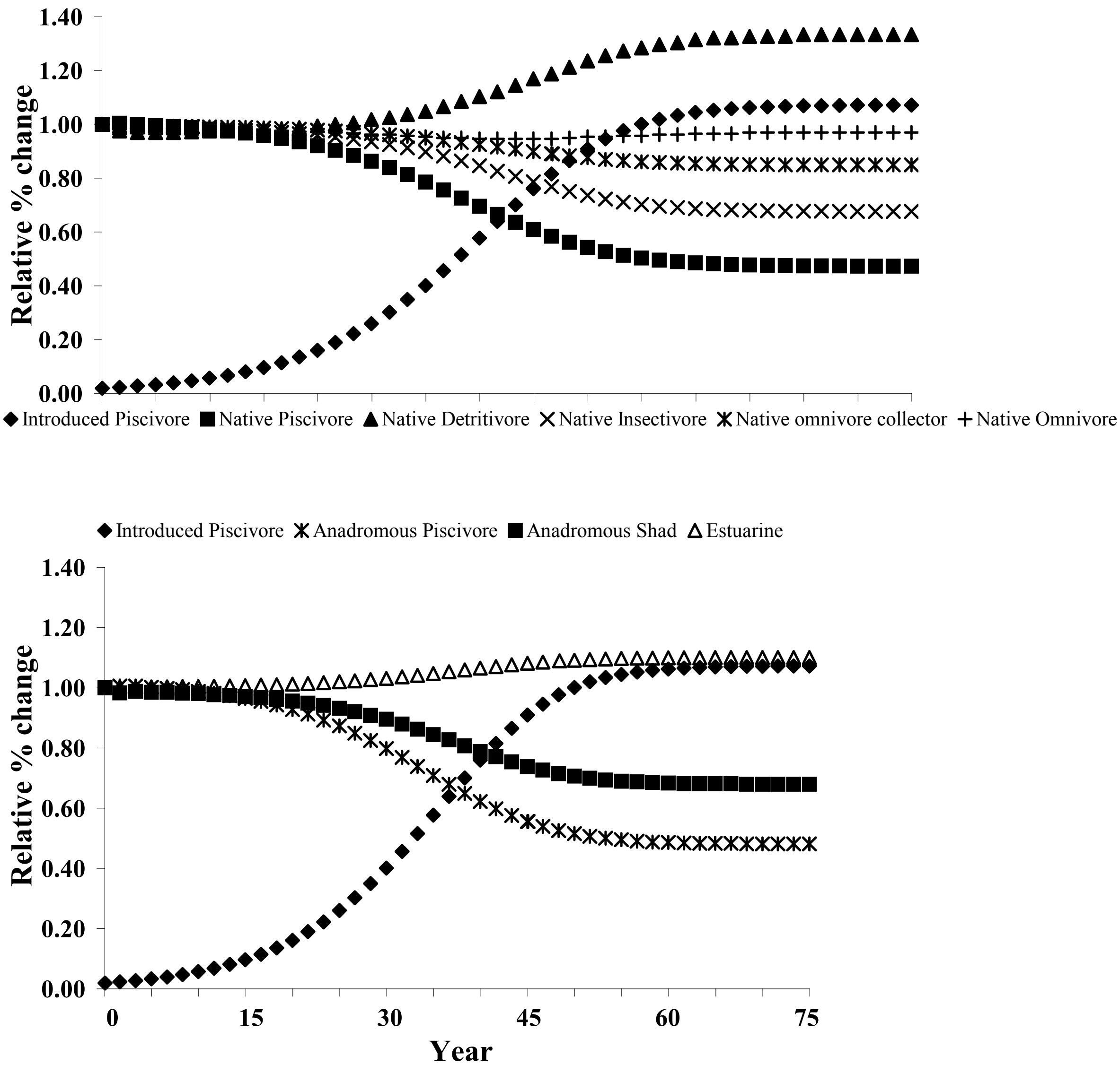
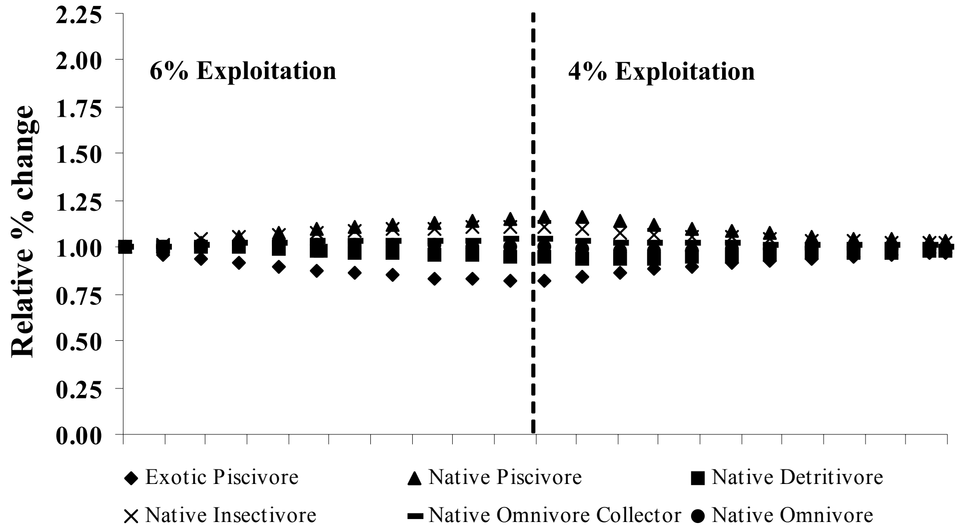


Figure 2. Simulated ecosystem response to flathead catfish introduction in a coastal river. Response is measured as change in the relative percent biomass of each fish functional group. Initial flathead catfish biomass in this simulation is the same as the biomass of the original North Carolina introduction (see text). Top panel is freshwater fish species and bottom panel is estuarine and anadromous species.



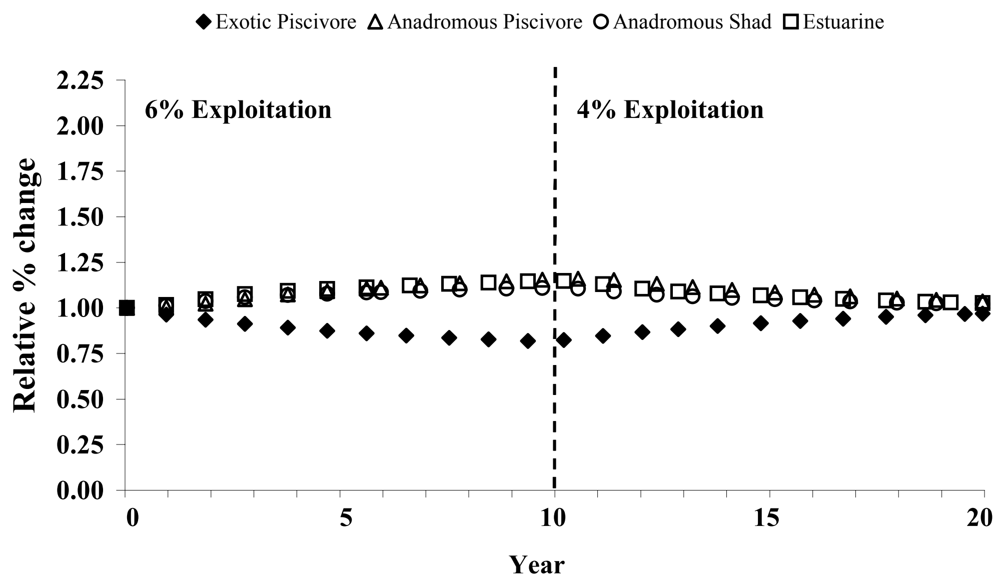
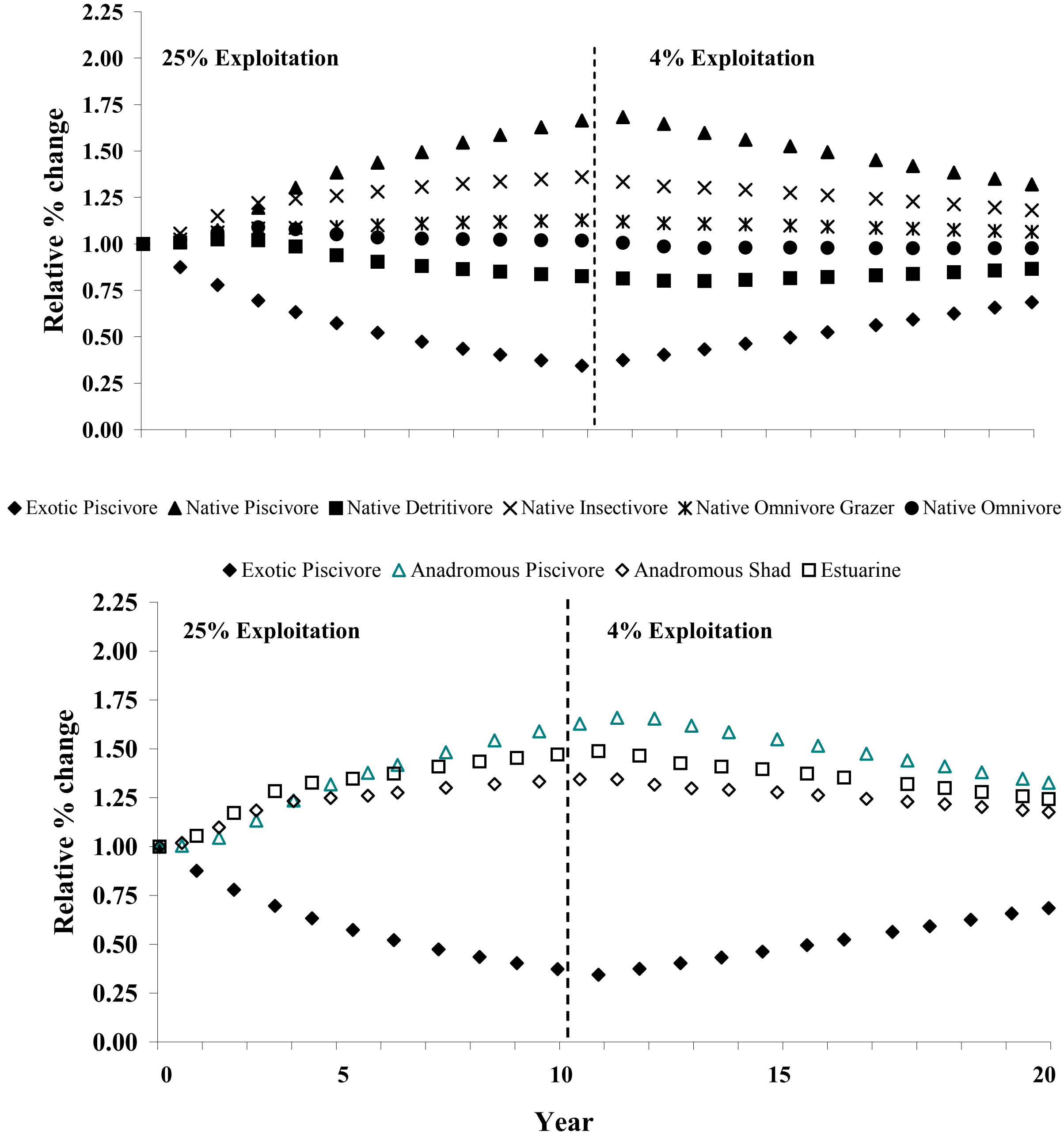


Figure 3. Relative percent change in biomass of freshwater, estuarine, and anadromous fish groups to changes in flathead catfish exploitation rates over a 20-year period. Simulated exploitation levels of 6 and 25% include the range or reported flathead catfish exploitation levels for native and introduced populations. Each exploitation level was applied for 10 years (left of dashed vertical line), and then exploitation was allowed to return to the current exploitation level (4%) for 10 years to monitor fish community response to changes in flathead catfish biomass (right of dashed line). Top panels are freshwater fish species and bottom panel is estuarine and anadromous species.



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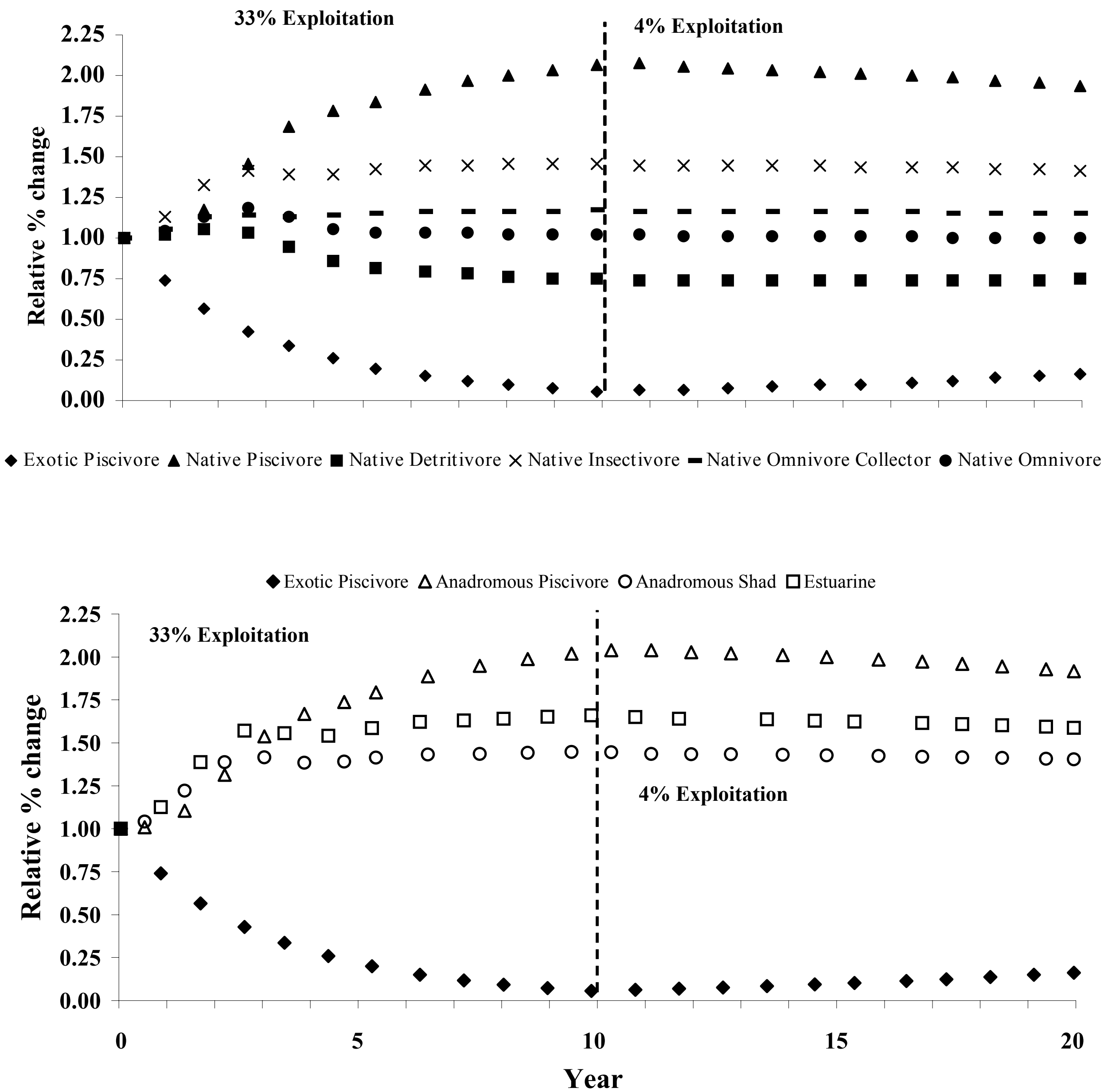
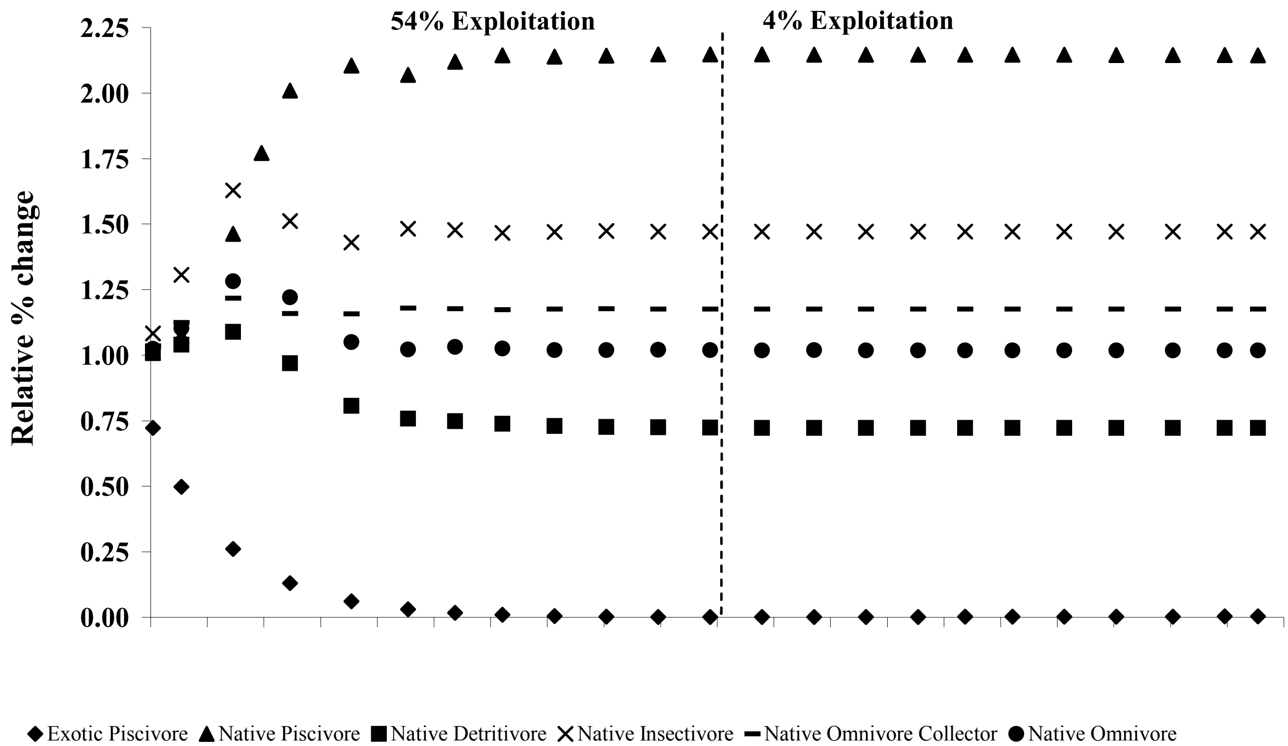


Figure 4. Simulated ecosystem response to flathead catfish eradication attempt through intensive exploitation measured as relative percent change in biomass of freshwater, estuarine, and fish. Exploitation levels of 33 and 54% were applied representing a 10 or 20 fold increases in exploitation from current levels. Intensive exploitation was applied for 10 years (left of dashed vertical line) then allowed to return to current exploitation levels (1x) for 10 years to monitor fish community response to changes in flathead catfish biomass (right of dashed line). Top panels are freshwater fish species and bottom panel is estuarine and anadromous species.



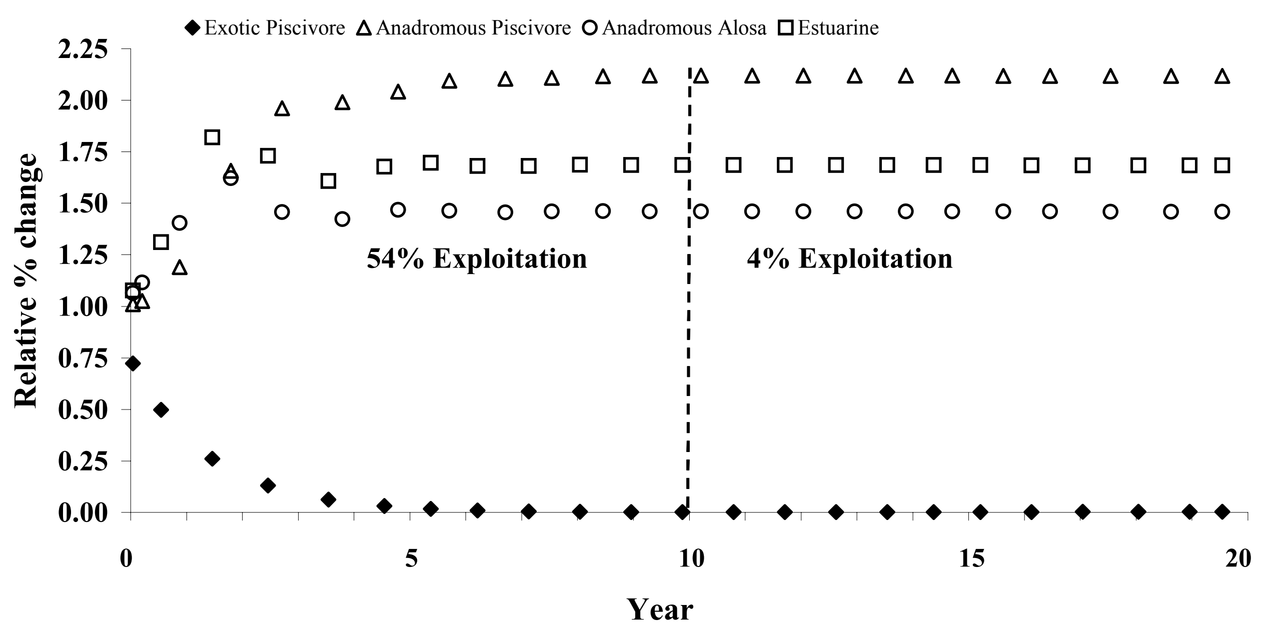
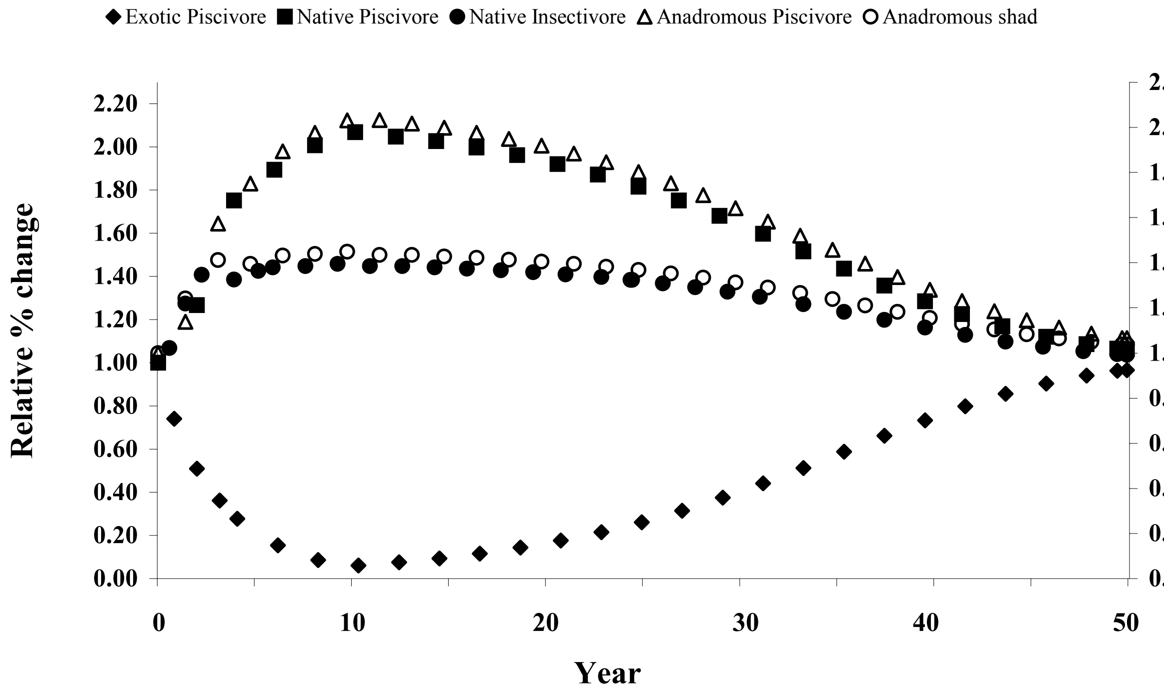


Figure 4 continued.



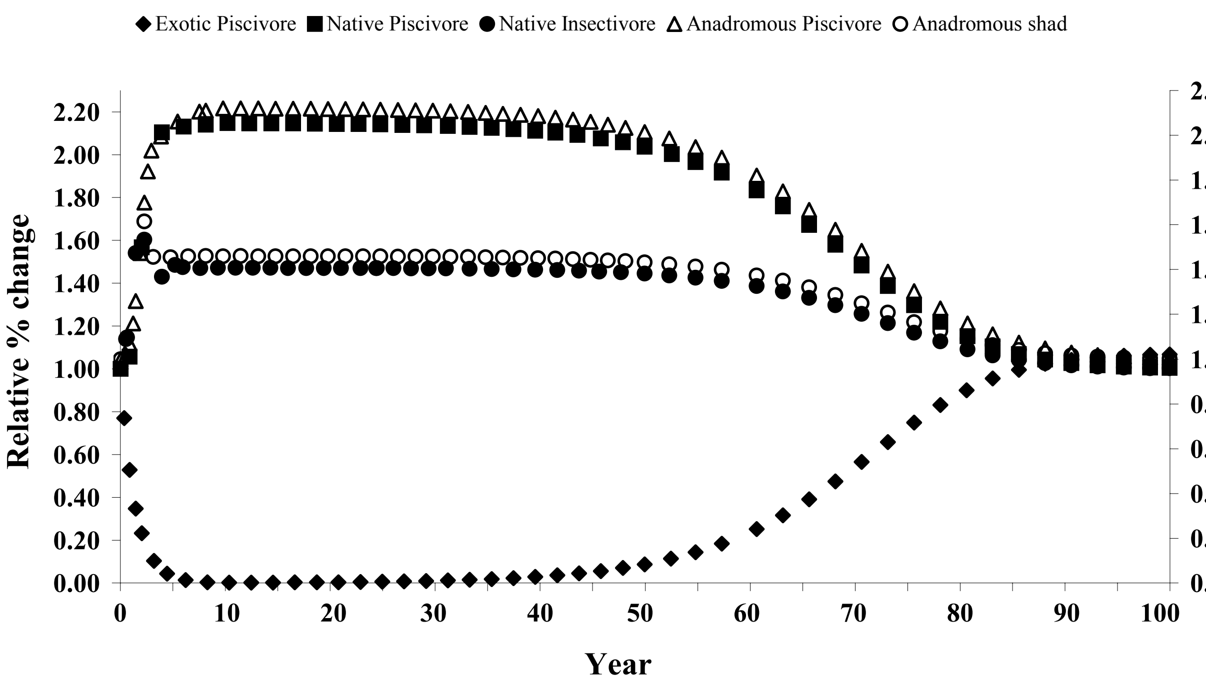


Figure 5. Simulated resiliency of flathead catfish of flathead catfish populations to intensive exploitation. Flathead catfish populations were exploited at high levels (33% and 54%) for 10 years and then populations monitored to determine whether populations would recover following intensive exploitation.

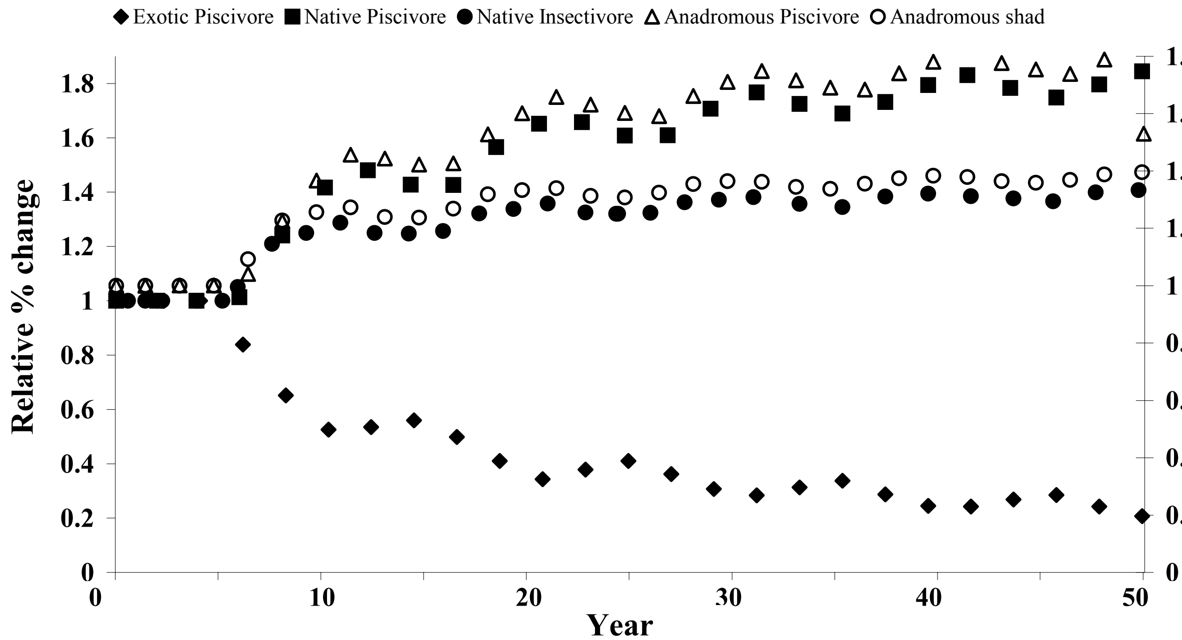


Figure 6. Maintenance control simulation demonstrating the response of native fish groups to oscillating levels of flathead catfish exploitation. Exploitation was held at the current level (4%) for five years, and then alternated between high (25%) and low (6%) exploitation levels for 5 years each for a total of 45 years. Relative percent change in biomass of freshwater fish species is on Y-axis 1, anadromous species on Y-axis 2.

Appendix 1. Estimating population biomass of each functional group.

Population estimates for each functional group were calculated by summing three-pass removal estimates for each species within that functional group. Often, removal estimates for an individual species were not possible because catch did not decline with each sampling pass (as required in a removal estimate, [Seber 1982]). However, at the functional group level there was usually a decline in group abundance among sampling passes. I combined the catch of each species, in each pass, within a functional group to create a three-pass "overall group removal." I then used this combined removal to estimate capture probability for that functional group. I then fixed capture probability for each species within the group to the group-wide capture probability and re-ran the removal model (using a closed capture model in program MARK) to estimate population size. Population biomass for each functional group (used in the Ecopath model) was then calculated by assigning an average weight (based on field measurements) to each species within the functional group, and then calculating a weighted average biomass for that functional group, weighted by the abundance of the individual members of the functional group (see text).

Appendix Table 1. Species name, functional group, functional group capture probability, number of individuals of each species caught in each pass, sum of catch from the three passes, estimated population size (fish/km), and standard error for each removal in Contentnea Creek

Appendix Table 1.

Contentnea Creek **Spring removal sample**							Population Size (fish/km)	
Species	Functional group	Capture probability	Pass 1	Pass 2	Pass 3	Sum All Passes	N	SE
Black crappie	Native piscivore	0.27	2	1	1	4	15	5.1
Bluegill sunfish	Native insectivore	0.27	33	27	31	91	371	24.3
Bowfin	Native piscivore	0.47	19	7	9	35	102	6.7
Channel catfish	Native omnivore	0.15	4	6	4	14	89	19.0
Creek chubsucker	Native omnivore	0.69	24	0	2	26	66	2.3
Chain pickerel	Native piscivore	0.47	3	1	1	5	13	2.6
Comely shiner	Native omnivore-grazer	0.05	0	0	1	1	16	16.2
Eastern mudminnow	Native omnivore-grazer	0.05	1	0	0	1	16	16.2
Eastern silvery minnow	Native omnivore-grazer	0.05	341	92	223	656	656	.
Gizzard shad	Native detritivore	0.45	0	0	3	3	8	.
Glassy darter	Native omnivore-grazer	0.05	0	0	1	1	16	16.2
Hogchoker	Estuarine	.	2	1	0	3	.	.
Longnose gar	Native piscivore	0.47	15	5	3	23	66	5.4
Largemouth bass	Native piscivore	0.47	20	16	4	40	116	7.2
Mosquitofish	Native insectivore	0.05	0	2	0	2	34	23
Pirate perch	Native omnivore-grazer	0.05	3	0	0	3	51	28.1
Pumpkinseed sunfish	Native insectivore	0.27	3	0	1	4	15	5.1
Redbreast sunfish	Native insectivore	0.27	22	11	9	42	171	16.5
RedbreastxBluegill sunfish hybrid	Native insectivore	0.27	1	0	0	1	3	2.6
Redear sunfish	Native insectivore	0.27	43	26	19	88	359	23.9
Redfin pickerel	Native piscivore	0.47	1	0	0	1	3	0.0
Sawcheek darter	Native omnivore-grazer	0.05	0	1	0	1	16	16.2
Shield darter	Native omnivore-grazer	0.05	1	2	2	5	86	36.3
Satinfin shiner	Native omnivore-grazer	0.05	21	25	25	71	1243	136.8
Shorthead redhorse	Native detritivore	0.45	4	0	1	5	14	2.8
Silver redhorse	Native detritivore	0.45	2	0	0	2	5	0.0
Striped bass	Anadromous piscivore	0.47	1	0	0	1	3	0.0
Swallowtail shiner	Native omnivore-grazer	0.05	19	6	6	31	542	90.4
Tesselated darter	Native omnivore-grazer	0.05	8	2	6	16	279	64.9

Appendix Table 1 continued.

Contentnea Creek **Fall removal sample**							Population Size (fish/km)	
Species	Functional group	Capture probability	Pass 1	Pass 2	Pass 3	Sum All Passes	N	SE
American shad	Anadromous shad	.	0	2	3	5	.	.
Bluegill sunfish	Native insectivore	0.25	13	10	9	32	137	15.9
Bowfin	Native piscivore	.	0	2	2	4	.	.
Channel catfish	Native omnivore	.	2	1	2	5	.	.
Creek chubsucker	Native omnivore	.	7	0	0	7	.	.
Coastal shiner	Native omnivore-grazer	0.06	0	3	1	4	58	27.0
Eastern silvery minnow	Native omnivore-grazer	0.06	5	26	47	78	1150	118.8
Gizzard shad	Native detritivore	0.43	0	1	0	1	3	0.0
Hickory shad	Anadromous shad	.	7	0	0	7	.	.
Largemouth bass	Native piscivore	0.48	18	13	7	38	109	6.8
Longnose gar	Native piscivore	0.48	1	3	2	6	15	0.0
Mosquitofish	Native insectivore	0.25	1	1	4	6	25	7.0
Mullet	Esturarine	.	1	1	1	3	.	.
Pirate perch	Native omnivore-grazer	0.06	1	0	0	1	14	13.5
Redbreast sunfish	Native insectivore	0.25	15	14	19	48	206	19.5
Redear sunfish	Native insectivore	0.25	11	8	13	32	137	15.9
Sawcheek darter	Native omnivore-grazer	0.06	1	0	1	2	28	19.0
Shield darter	Native omnivore-grazer	0.06	3	0	10	13	191	3.5
Satinfin shiner	Native omnivore-grazer	0.06	1	6	2	9	132	40.3
Shorthead redhorse	Native detritivore	0.43	3	2	2	7	20	3.5
Silver redhorse	Native detritivore	0.43	1	1	0	2	5	0.0
Tesselated darter	Native omnivore-grazer	0.06	2	9	20	31	456	74.9
Warmouth	Native insectivore	0.25	0	1	0	1	3	0.0

Appendix Table 2. Model parameter estimates used in the mass-balance Ecopath model.

Functional group name	Biomass in habitat area (t/km²)	Source
Exotic piscivore	0.237	This study
Native piscivore	0.165	This study
Native detritivore	0.022	This study
Native insectivore	0.185	This study
Native omnivore collector	0.390	This study
Native omnivore	0.025	This study
Anadromous piscivore	0.003	This study
Anadromous shad	0.035	This study
Estuarine	0.015	This study
Invertebrates	4.000	Range from Waters 1977
Plankton	1.000	Range from literature
Detritus	100.00	Range from literature

Functional group name	Production/ biomass	Source
Exotic piscivore	0.150	This study, catch-curve
Native piscivore	1.050	This study, multiple 3-pass removals
Native detritivore	1.750	This study, multiple 3-pass removals
Native insectivore	2.800	This study, multiple 3-pass removals
Native omnivore collector	1.890	This study, multiple 3-pass removals
Native omnivore	1.750	This study, multiple 3-pass removals
Anadromous piscivore	2.000	This study, multiple 3-pass removals
Anadromous shad	2.200	This study, multiple 3-pass removals
Estuarine	2.600	This study, multiple 3-pass removals
Invertebrates	5.500	Range from Waters 1977
Plankton	35.000	Range from literature
Detritus	-	

Functional group name	Consumption/ biomass (per year)	Source
Exotic piscivore	3.600	Fishbase
Native piscivore	3.930	Fishbase
Native detritivore	14.100	Fishbase
Native insectivore	10.000	Fishbase
Native omnivore collector	36.700	Fishbase
Native omnivore	4.800	Fishbase
Anadromous piscivore	6.000	Fishbase
Anadromous shad	5.000	Fishbase
Estuarine	10.000	Fishbase
Invertebrates	16.500	Fishbase
Plankton	-	Not estimable
Detritus	-	Not estimable

Appendix Table 2 continued.
Diet percent-composition for each functional group. Exotic piscivore functional group information is based on diet samples collected in this study, while other groups are estimated from the literature.

	Exotic piscivore	Native piscivore	Native detritivore	Native insectivore	Native omnivore-collector	Native omnivore	Anadromous piscivore	Anadromous shad	Estuarine	Invertebrates	Plankton	Detritus
Exotic piscivore	0.0%	0.4%	0.4%	35.0%	31.0%	1.2%	0.0%	5.0%	2.5%	24.5%	0.0%	0.0%
Native piscivore	0.0%	10.0%	5.0%	27.5%	20.0%	5.0%	0.0%	5.0%	2.5%	25.0%	0.0%	0.0%
Native detritivore	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	100.0%
Native insectivore	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	50.0%	40.0%	10.0%
Native omnivore-collector	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	40.0%	40.0%	20.0%
Native omnivore	0.0%	0.0%	0.0%	5.0%	5.0%	0.0%	0.0%	0.0%	0.0%	50.0%	0.0%	40.0%
Anadromous piscivore	0.0%	0.0%	10.0%	25.0%	35.0%	5.0%	0.0%	0.0%	5.0%	20.0%	0.0%	0.0%
Anadromous shad	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	80.0%	20.0%
Estuarine	0.0%	0.0%	0.0%	0.0%	20.0%	0.0%	0.0%	0.0%	0.0%	40.0%	10.0%	30.0%
Invertebrates	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	100.0%

Appendix Table 2 continued.

Functional group name	Diet information source
Exotic piscivore	This study
Native piscivore	Davies 1981; Fishbase
Native detritivores	Fishbase
Native insectivore	Fishbase
Native omnivore-collector	Fishbase
Native omnivore	Fishbase
Anadromous piscivore	Neal et al. 1999; Fishbase
Anadromous shad	Fishbase
Estuarine	Fishbase
Invertebrates	Assumed
Plankton	Assumed
Detritus	Not estimable

CHAPTER 6

SYNTHESIS AND DIRECTION OF FUTURE RESEARCH

Synthesis

Based on the results presented in this dissertation, I conclude that introduced flathead catfish populations in North Carolina have likely altered native fish community biomass through both predatory and competitive interactions. I developed this conclusion based on estimates of flathead catfish population size (Chapters 2, 3), diet information (Chapter 4), and simulation models based on empirical diet information, native fish community composition and abundance, and flathead catfish exploitation levels from native populations (Chapter 5). I found that flathead catfish population size in coastal North Carolina rivers can be assessed using a robust design population model as outlined in Chapters 2 and 3. The robust design model performed well because I was able to account for temporary emigration by flathead catfish, which would not be possible with closed or open population models. Population size estimates for flathead catfish in my study (4-31 fish/km) were within the broad range of sizes previously reported for both native and introduced riverine populations (Chapter 3). Estimated population size of introduced flathead catfish populations in the coastal North Carolina rivers I examined are smaller than in other introduced populations in the southeastern US (Chapter 3).

I found that in coastal North Carolina rivers, flathead catfish are strict, obligate carnivores that mainly feed on other fishes and crayfish. When available, flathead catfish also utilize marine derived fish and invertebrate food resources. The use of these resources by flathead catfish could be particularly important in planning restoration efforts for anadromous species in coastal rivers with flathead catfish populations.

I combined demographic information for flathead catfish and the native fish community, with diet information for both groups, in an ecosystem simulation model to examine the interactions between flathead catfish and the native fish community. These simulation models indicate that flathead catfish have altered native fish communities via both direct predation of, and indirect competition with, native fishes. However, these impacts might be mitigated through intensive harvest of flathead catfish at levels similar to those found for native flathead catfish populations, about 10-25%.

Aquatic Invasion Rules

Moyle and Light (1996) developed a series of empirical “rules” to predict the fate of species introduced in stream and estuarine environments. Although originally derived for California waters, several of these rules appear to characterize the flathead catfish invasion along the Atlantic slope. I review these rules below as a framework in which to summarize my findings and describe areas of future research that could be used to develop testable hypotheses to further our understanding of invasive species in aquatic environments.

Moyle and Light (1996) Rule: Most invaders fail to become established.

While most invasions fail, those that have been successful are often predators (particularly piscivores) (Moyle and Light 1996). Flathead catfish are well established in the coastal rivers I examined as evident by the range of sizes collected and population size estimates. Given the low detectability for flathead catfish in coastal rivers (Chapter 3), they may be established elsewhere, but not yet detected.

Moyle and Light (1996) Rule: In the long term, or in relatively undisturbed aquatic systems, success of an invader will depend on a close match between its physiological and life history requirements and the characteristics of the system being invaded.

Many invasive fish species are part of a small group of widely and frequently introduced sportfish, including flathead catfish (Moyle 1986; Heidinger 1993; Moyle and Light 1996). These sportfish species have successfully invaded new systems and established self-sustaining populations not because of some intrinsic adaptability of these species, but instead, their success is a function of the frequency which they have been introduced and the successful pairing of the introduced species with the environment in which it is released– often by well meaning anglers or management agencies (Moyle 1986; Moyle and Light 1996).

Moyle and Light (1996) Rule: Most successful invaders are integrated without major negative effects (e.g., extirpations) on the communities being invaded.

While I have no evidence of any native fish species extirpations related to direct predation by flathead catfish within the rivers I studied, I was able to demonstrate (via simulation modeling, Chapter 5) that flathead catfish have probably caused reductions in native fish biomass via both competitive and predatory interactions (Chapters 4, 5). Invasive piscivorous fish have been shown to alter native fish assemblages in other systems (White and Harvey 2001), and although my results are derived from simulations, they provide guidance into how the native fish community would respond to reductions in flathead catfish biomass through intensive exploitation– a widely considered management action for introduced flathead catfish populations.

Moyle and Light (1996) Rule: Major community effects of invasions are most often observed where the number of species is low.

The impact on native fish communities following flathead catfish introduction may primarily be a function of the type of system into which they are introduced. Thus, the greatest impact of flathead catfish predation likely occurs in relatively unproductive systems (e.g., small streams and rivers, many with few species) while their impact may not be as noticeable in larger systems with more species. This rule was originally developed for high mountain California streams with only 5-7 fish species, but it may apply here in systems with more (20-30) species. The availability of anadromous and estuarine food items for flathead catfish in Contentnea Creek and the Northeast Cape Fear River may lessen the impact of flathead catfish predation on native fishes as compared to that in the Lumber River. These marine based prey items may serve as flathead catfish predation buffers to the native fish community. Thus, flathead catfish in the Lumber River, with fewer available prey species, may concentrate their feeding pressure on a smaller group of species, potentially causing greater change to the native fish community and making their impact more readily apparent (Chapters 4, 5).

Moyle and Light (1996) Rule: In aquatic systems with intermediate levels of human disturbance, any species with the right physiological and morphological characteristics can become established.

Flathead catfish are not the only aquatic invasive species in each of these river systems. Several of the identifiable prey items in my study and that of Guier et al. (1981) were themselves introduced species into the mid-Atlantic slope. These species included redear sunfish, blue catfish, and flathead catfish. The Neuse River drainage supports 20 aquatic invasive species, the Cape Fear River drainage contains 31, while the Little Pee Dee "only" supports 11. Disturbed aquatic ecosystems are more likely than undisturbed systems to support invasive species (Moyle and Light 1996). Both the Neuse and the Northeast Cape Fear rivers are anthropogenically impacted rivers (nutrient enrichment, sedimentation, flow regime alterations; Cahoon et al. 1999; Paerl et al. 2001), while large portions of the Lumber River retain "National Wild and Scenic River" status from the US National Park Service for their relatively pristine condition.

Future Research

My simulation results suggesting positive responses in native fish biomass following flathead catfish harvest could be considered as a part of a broader ecosystem restoration effort to mitigate the variety of anthropogenic ecosystem alterations in coastal rivers. While many aspects of coastal river ecosystem restoration remain in an experimental phase (Lenihan et al. 1999), our ability to harvest fish populations is well established, and directed harvest toward flathead catfish may represent a conceptually simple, but important step in helping restore degraded ecosystems. Interest in flathead catfish as a sportfish within both native and introduced river systems is growing as evident by the increasing number of popular press publications devoted to this species, increasing specialization among angler groups (including tournaments), and the creation of specialized fishing equipment designed to target large catfish (Quinn 1993; Jackson 1999). Efforts should be made to encourage these developing fisheries and to monitor angler effort, expectations, and ecosystem response to flathead catfish harvest. Future research along the Atlantic slope should also focus on understanding the linkages flathead catfish create between marine and freshwater foodwebs. Efforts should also be made to determine if in the absence of marine derived food resources, flathead catfish have a greater impact on native fish communities.

Flathead catfish are a remarkable animal, capable of eliciting excitement, and even respect, from both resource users and managers in native and introduced ecosystems. These attitudes towards an animal with few charismatic qualities (to some) may stem largely because of their ability to attain large physical size, potential to restructure ecosystems, and maybe even from the mystery that surrounds large aquatic animals that we cannot readily see and do not completely understand. Although my research has provided new information on this species in coastal North Carolina rivers, much remains to be learned about this amazing creature by future researchers fortunate to work with this species.

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