POPULATION DYNAMICS OF SMALLMOUTH BASS IN THE BEAVER ARCHIPELAGO, NORTHERN LAKE MICHIGAN, 1999-2002

by

MICHAEL JOHN SEIDER

Under the Direction of Douglas L. Peterson

ABSTRACT

The Beaver Island Archipelago in Lake Michigan had a popular smallmouth bass (*Micropterus dolomieui*) fishery in the 1970-80s. In the 1990s, anglers became concerned that the smallmouth bass population was in decline due to predation by the increasing double-crested cormorant (*Phalacrocorax auritus*) population in the archipelago. The objective of this study was to determine the status of smallmouth bass by estimating current population characteristics and comparing them to past data. I estimated population size, condition, growth, and cohort survival for smallmouth bass from 1999-2002. Smallmouth bass abundance had declined 85-92% since the 1970-80s. Growth rates and condition had increased since the 1970s. High adult survival and similar declines in nongame fish species indicated that angler harvest was not limiting smallmouth bass abundance. Mortality rates for ages 3-5 were as high as 99%, which is consistent with cormorant predation. These data suggested that cormorant predation is limiting smallmouth bass abundance.

INDEX WORDS: Smallmouth Bass, Lake Michigan, Beaver Archipelago, Double-Crested Cormorants, Population Estimates, CAPTURE, Age-Specific Mortality, Relative Weight, von Bertalanffy Growth Equation

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DEDICATION

To John and Karen Seider for encouraging me to pursue my passion for science.

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CHAPTER 1

INTRODUCTION

Biology of the Smallmouth Bass

Identification

The smallmouth bass (*Micropterus dolomieui*, hereafter: smb) (Figure 1) is one of seven species of black basses in the family Centrarchidae. The black basses exhibit similar morphology and early naturalists often misidentified several species. Diagnostic characteristics of smb are: (1) upper jaw does not extend beyond posterior edge of eye, (2) gill rakers on first gill arch long, straight, and pointed, and (3) two dorsal fins joined and appear as one; first dorsal fin with 10 spines, second with 13-15 soft rays (Becker 1983). Although adult smb coloration varies, generally, their dorsal region is brown, yellow-brown, or green with a yellow/white underside (Becker 1983). External features such as coloration cannot be used to precisely determine the age or sex of smb.

Distribution/Habitat

The geographic distribution of smb has expanded in the last century. Before 1900, smb were found only in North America from Minnesota and the Great Lakes south to northern Georgia, and west to Oklahoma (Coble 1975; Figure 1). However, smb have been stocked and naturalized in lakes and rivers throughout the continental United States and Canada, as well as in Hawaii, Asia, Africa, Europe, and South America.

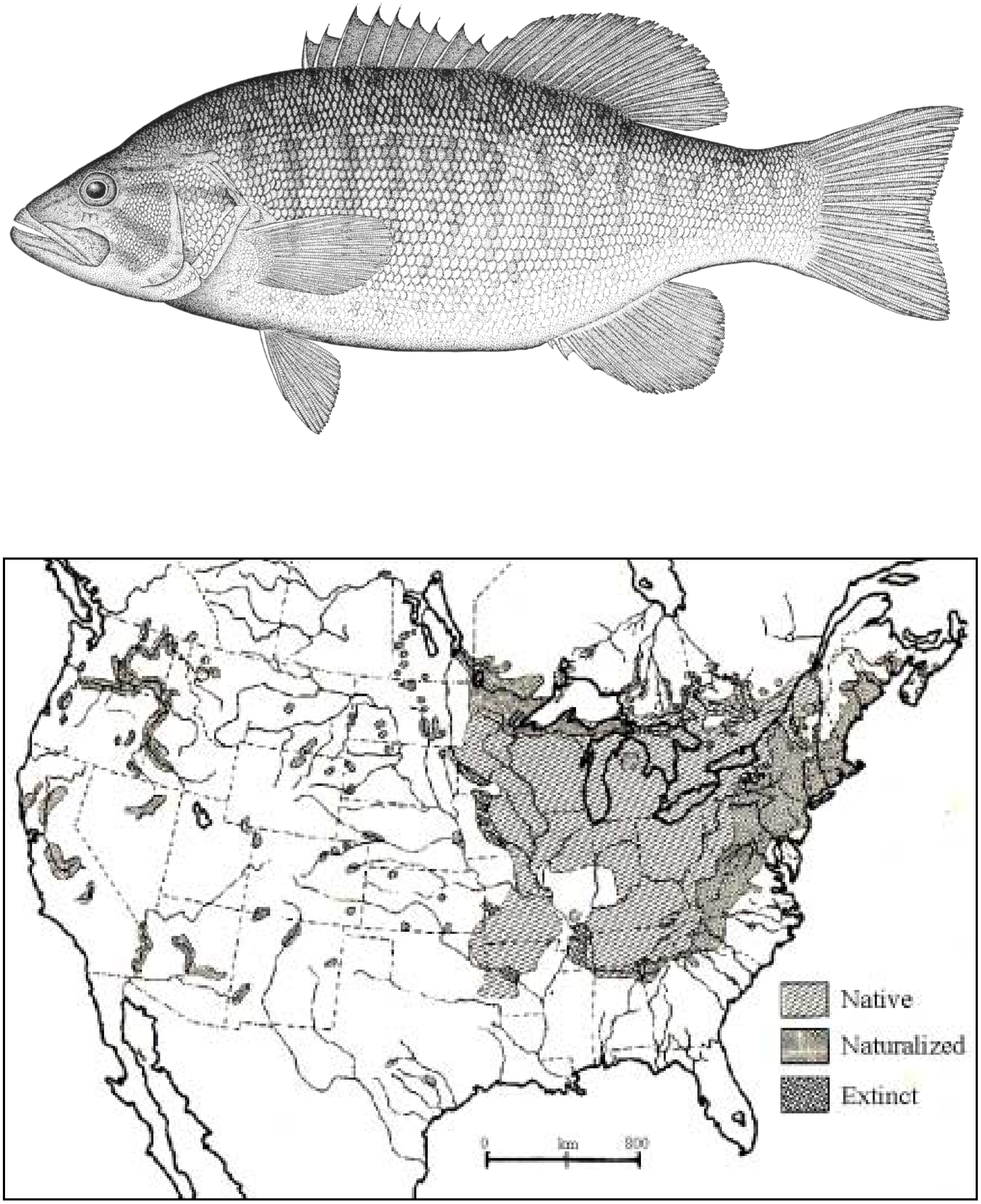

Figure 1. Native and naturalized distribution of smallmouth bass (*Micropterus dolomieui*) in North America from Coble (1975). Illustration of smallmouth bass by Paul Vecsei.

Smallmouth bass are found in a wide range of habitats. Typically, these include large lakes or cool, clear streams, but they also live in small ponds and turbid streams (Coble 1975). Smallmouth bass prefer habitat with rock, sand, or gravel substrate, largerock or submerged trees, and summer water temperatures between 21.1-26.7ºC (Becker 1983). In summer, they rarely inhabit water deeper than 12 m and are often found at depths of 2-6 m. Summer habitat preference, however, may be related to the total length of smb. Cole and Moring (1997) found that large smb (>406 mm) inhabited deeper water (4-8 m) while smaller smb (248-279 mm) were associated with cover in shallow water. In autumn, smb congregate in deeper water as temperatures drop below 10ºC (Coble 1975).

Reproduction

Smallmouth bass spawning in the Great Lakes occurs in shallow water during May and June when water temperatures reach 16ºC (Coble 1975). Smallmouth bass in Lake Michigan become sexually mature at age 6-8 (females usually spawn one year later than males) (Becker 1983). Before spawning, the male smb excavates a nest in gravel, rubble, or sand substrate in water depths of 0.4-1.5 m (Becker 1983). The nests usually are found along sheltered shorelines, probably because high wind and waves reduce spawning success (Goff 1986). Spawning is initiated by an elaborate courtship behavior displayed by the male and female, after which the female deposits 1000-11,000 eggs in the nest (Coble 1975; Raffetto et al. 1990). The male then fertilizes the eggs and guards the nest for up to four weeks to protect its eggs and fry from predation (Becker 1983).

Diet

Smallmouth bass go through several ontogenetic shifts as they grow. As their yolk sac diminishes, larval smb begin feeding on zooplankton such as copepods and cladocera (Coble 1975). As young juveniles their diet may include insects, such as ephemeropterans and odonates (Becker 1983). Weidel et al. (2000) found that older juveniles switch from feeding on insects to crayfish (Order Decapoda) and small fishes as they approach 150 mm total length (TL). Adults may consume minnows (Family Cyprinidae), darters (Family Percidae), alewife (*Alosa pseudoharengus*) (in the Great Lakes), and crayfish (Coble 1975; Becker 1983; Stephenson and Momot 1991; Long and Fisher 2000; Weidel et al. 2000).

Background on the Fishery

The Beaver Island Archipelago in northeastern Lake Michigan was once home to a popular smb fishery. In the 1970s, the fishery was revealed by publications such as *Field & Stream* (Smith 1975). The publicity created a valuable tourist attraction for the local economy and; according to local residents the Archipelago annually attracted thousands of anglers throughout the 1970s and 1980s. By 1990, however, angler interest waned as smb catches declined. Concerned over the future of the fishery, island citizens contacted the Michigan Department of Natural Resources (MDNR). Although most island residents believed double-crested cormorant (*Phalacrocorax auritus*, hereafter: cormorants) predation had caused a smb decline, supporting scientific evidence was lacking. The MDNR had not surveyed the Beaver Island fish community and only limited historical data were available (H.L. Lenon, unpublished data).

Potential Causes of Suspected Smallmouth Bass Decline

The primary goal of this study was to assess the status of smb in the Beaver Islands and, subsequently, to provide biological data that might help determine why the fishery had declined. Without current data on the local smb populations, causes of the fishery decline were merely speculative. Based on the anecdotal evidence from local residents and limited historical data however, the three most probable causes of the suspected decline were ecological disturbance, recreational angling, and cormorant predation.

Effects of recent ecological changes on the smallmouth bass fishery

The Great Lakes have experienced constant ecological disturbance over the last 200 years (Bogue 2000). The most recent disturbance was caused by introductions of several exotic species including the zebra mussel (*Dreissena polymorpha*), the ruffe (*Gymnocephalus cernus*), two species of goby (Family Gobidae), and an exotic zooplankton (*Bythotrephes cederstroemi*). Although the cumulative effect of these invasions is uncertain, the resources available (e.g. food, habitat) to native fishes likely have been altered (Jude and Leach 1999). A reduction in food availability in the Beaver Archipelago would cause slower growth and poor condition for smb. Furthermore, if the reduction were severe, smb abundance could be decreased by starvation, disease or poor recruitment.

Effects of recreational angling on the smallmouth bass fishery

Several researchers have shown that recreational angling can adversely affect smb survival and reproduction (Kiefer et al. 1995; Philipp et al. 1997; Ridgway and Shuter 1997). Angler harvest may limit smb abundance by removing most individuals longer than the minimum length limit, thus reducing the spawning stock. Harvest during the spawning period may cause further damage by removing adults from their nests, which directly reduces reproductive success (Kiefer et al. 1995; Ridgway and Shuter 1997). Because males are more aggressive when guarding their nests (Philipp et al. 1997), they are often more vulnerable to angling. Therefore, beginning in 2001 the MDNR closed the smb season until 1 July in the Beaver Archipelago, to protect smb during the spawning period.

Although the closed season prevents legal harvest during the spawning period, catch-and-release angling may still affect the reproductive success of smb. Male smb removed from the nest by anglers become physiologically stressed after the struggle (Shreer et al. 2001). Stressed males may return slowly to their nests or in some instances abandon their offspring, which can ultimately decrease annual recruitment (Kiefer et al. 1995; Ridgway and Shuter 1997). Catch-and-release angling can reduce the reproductive success of individual smb, but studies indicating it decreases reproductive success at the population level are lacking (Philipp et al. 1997). Catch-and-release angling after the spawning season also may indirectly affect smb population size because angling struggle often causes an extended period of stress or injury that may reduce smb fitness and survival after the fish has been released (Shreer et al. 2001).

Effects of cormorant predation on the smallmouth bass fishery

Biology of cormorants in the Great Lakes

Cormorants are piscivorous, diving birds that often feed in water less than 10 m deep (Custer and Bunck 1992). Typically, they travel less than 20 km from the nesting colony to forage and they usually forage in habitat within 3 km of shore (Neuman et al.

1997; Stapanian et al. 2002). Cormorants may consume 0.25-0.5 kg of fishes each day, with those fishes primarily ranging from 50-300 mm TL (Shramm et al. 1984; Craven and Lev 1987; Hobson et al. 1989; Shramm et al. 1989; Campo et al. 1993; Modde et al. 1996; Neuman et al. 1997; Adams et al. 1999; Johnson et al. 2001; Johnson et al. 2002). Diet composition of cormorants varies depending on the relative abundance of fish species in the environment. In the Great Lakes, abundant forage fishes such as the exotic alewife usually constitute the vast majority of the birds' diet compared to other fishes such as yellow perch (*Perca flavescens*), catfishes (Family Ictaluridae), rockbass (*Ambloplites rupestris*), and smb (Craven and Lev 1987; Hobson et al. 1989; Ludwig et al. 1989; Weseloh and Ewins 1994; Neuman et al. 1997).

Cormorants nest throughout the Great Lakes from mid-April through September. Typically, they build nests nest in trees or on the ground in dense colonies on small rocky islands (Weseloh and Ewins 1994). Once the nests are constructed, females lay 3-5 eggs that are incubated by both parents for 25-29 days (Orta 1992). Chicks remain in the nest for up to 42 days and are provided regurgitated food (by parents) until they can fly and feed independently.

Historical changes in cormorant abundance in the Great Lakes

Cormorant abundance has fluctuated widely in the Great Lakes since European settlement. Lewis (1929) suggests that migrating cormorants were common on the Great Lakes during the early 1800s, however they were rarely observed by the late nineteenth century (Barrows 1912). The first confirmed nesting pair of cormorants was observed on Lake Superior in 1913 (Weseloh 1996). By 1950, they had increased to about 900 nesting pairs in the Great Lakes (Weseloh 1996). From 1950 to 1970, cormorants were reduced to less than 100 nesting pairs by the widespread use of DDT that caused eggshell thinning and hatchling deformities (Weseloh et al. 1983).

Federal protection from hunting, a ban on DDT, and the availability of the introduced alewife as an abundant new food source probably allowed Great Lakes cormorant populations to recover over the last 30 years. In fact, populations have increased at an average annual rate of 29% since 1975 (Weseloh et al. 1995). Nesting pairs of cormorants in the Great Lakes have increased from 98 in 1973 to approximately 115,000 in 2000 (Weseloh et al. 2000). A similar increase has occurred in Michigan, where nesting pairs have increased from 24 in 1978 to 25,758 in 1997 (Ludwig and Summer 1997). From 1989 to 1997, the number of nesting pairs just in the Beaver Archipelago increased from 880 to 11,709, an increase of more than 13 fold (J. Gillingham, Central Michigan University, pers. comm.).

Concerns for sport fisheries

The rapid increase of cormorants in the Great Lakes has become a public concern. Because cormorants are easily recognized fish predators, they have been blamed for the decline of many local fisheries. Articles in the *New York Times* and *Detroit Free Press* discussed the possible effects of cormorant predation on local fisheries in the Great Lakes and highlighted the public outcry (Sharp 2002; Wilgoren 2002).

Although previous cormorant diet studies found that gamefish did not constitute a large percentage of the birds' diet, the cumulative effect of predation on local fisheries is uncertain. As opportunistic feeders, the cormorants' diet is largely dependent on the relative abundance of fish species in the environment. Because gamefish species are typically less abundant than forage species, sportfish usually constitute a relatively small percentage of the cormorant diet (Craven and Lev 1987; Hobson et al. 1989; Ludwig et al. 1989; Neuman et al. 1997). Previous studies of Great Lakes cormorants have found that smb typically constitute less than 10% of prey biomass or total number of prey consumed (Ludwig et al. 1989; Neuman et al. 1997; Johnson et al. 2002). Although predation rates can be obtained through diet studies, the relative abundance of both predator and prey must be considered when evaluating the potential effect on a prey population.

Since the 1980s, the cormorant population within the Beaver Islands has grown to nearly 12,000 pairs, placing it among the largest in the Great Lakes (J. Gillingham, Central Michigan University, pers. comm.). Because each bird typically consumes about 0.25-0.5 kg fish per day (Shramm et al. 1984; Shramm et al. 1989), and spends approximately 180 days in the archipelago, a large proportion of the smb population could be consumed even if smb were to constitute less than one percent of the cormorant diet. For example, if every cormorant nesting in the Beaver Archipelago ate only one smb during an entire year, the cumulative effect of removing 25,000 individuals from the smb population could be devastating to the fishery.

During preliminary diet analyses of Beaver Archipelago cormorants, Gillingham and Seefelt (2001) found relatively large quantities of crayfish in cormorant stomachs. Although cormorants feed primarily on fish, several cormorant researchers have also reported crayfish remains in stomach samples, fecal pellets, and regurgitated material (Hobson et al. 1989; Ludwig 1989; Orta 1992; Neuman et al. 1997). Johnson et al. (1997) however, warns that some crayfish remains found in pellets originate from smb and rockbass consumed by cormorants. Consequently, when evaluating the importance of crayfish in cormorant diets, direct examination of cormorant stomach contents may be critical. For example, Gillingham and Seefelt (2001) found that crayfish might comprise as much as 24% of the stomach contents of cormorants feeding around the Beaver Archipelago. These findings may be important because crayfish are most abundant in the shallow water habitats where most smb are also found (Becker 1983). Therefore, large quantities of crayfish in cormorant diets may indicate that the birds were foraging in smb habitats.

In 1998, the New York State Department of Environmental Conservation (NYSDEC) and United States Geological Survey (USGS) began studying the effects of cormorants on fish populations in eastern Lake Ontario. Before that study, mean catch-per-unit-effort (CPUE) from gill net surveys for smb in the eastern basin had declined 50% from 1985 to 1995, while the relative abundance of smb in other regions of Lake Ontario did not change (Chrisman and Ekert 1999). Decreasing angler catch rates also coincided with the rapid increase of nesting cormorants in the region (<100 pairs in 1979 to approximately 8000 pairs in 1998) (Weseloh and Ewins 1994). Lantry et al. (2002) found that relative annual mortality of ages 3-5 smb increased from 0.4 in the 1970s and 1980s to 2.25 in the 1990s. Interestingly, Chrisman and Ekert (1999) found that individual growth rates for this smb population had increased since the 1980s, suggesting that ecological changes in Lake Ontario had not likely caused the smb decline. Furthermore, the increase in juvenile smb mortality was consistent with cormorant predation because adult smb are typically too large for cormorants to eat (Craven and Lev 1987; Hobson et al. 1989; Campo et al. 1993; Modde et al. 1996; Neuman et al. 1997; Adams et al. 1999; Johnson et al. 2001; Johnson et al. 2002). Johnson et al. (2002) also reported that smb constituted 0.7% of the cormorants' diet during the pre-nesting period, but during nesting, this increased to 3.7-7.2%. Based on nest counts and diet analyses, Ross and Johnson (1999) estimated that cormorants consumed between 130,000 and 750,000 smb annually in eastern Lake Ontario from 1993 through 1997. Unfortunately, absolute estimates of smb population size were not calculated during that period, hence the cumulative effect of cormorant predation on the smb fishery could not be quantified.

The rapid increase of cormorants in the Great Lakes has caused public concern for local fisheries. Some previous research on cormorants suggested that the birds did not affect gamefish populations. Most previous cormorant research however, relied solely on cormorant diet analyses to evaluate the birds' effect on local fisheries. Recent research on Lake Ontario quantified the characteristics of both cormorant and smb populations and found strong evidence that cormorant predation was having a significant effect on smb.

Objectives

The primary goal of this study was to determine the present status of the smb population in the Beaver Islands. By quantifying current population characteristics and comparing them to historical data, I hoped to identify factors that might be limiting smb numbers. The objectives of this study, then, were to estimate population size, to quantify cohort survival rates, and to evaluate growth and condition of smb in the Beaver Island Archipelago. Another objective was to estimate the population size of rockbass and brown bullhead (*Ameiurus nebulosus*) in the Archipelago.

First, smb population size was estimated to quantify changes in abundance over the last 30 years, by comparing these data with similar estimates conducted in the 1970s and 1980s. Changes in smb abundance since 1970 would indicate approximately when the fishery might have declined, indicating a potential cause. For example, if angler harvest had caused the supposed decline then smb abundance would have declined in the 1970s when the fishery was popular. Whereas the suggested smb decline would have begun in the early 1990s if cormorant predation were the primary cause.

Second, rockbass and brown bullhead abundance was estimated to determine the status of nongame fish species. Population estimates of these species from 1999 through 2002 were compared to similar estimates from 1984 to determine if they had declined. Because anglers rarely target rockbass and brown bullhead, a decline in these species would suggest that overharvest was probably not responsible for local fish declines. A decline of rockbass and brown bullhead abundance might also provide indirect evidence of cormorant predation in shallow water smb habitats because the birds commonly consume these species as well (Ludwig et al. 1989; Neuman et al. 1997; Schneider and Adams 1999).

Third, survival rates of smb were estimated to help reveal potential population bottlenecks that might limit smb abundance. For example, unusually high adult mortality might indicate that angler harvest was limiting smb abundance. On the other hand, high juvenile mortality might indicate that cormorant predation could be the most limiting factor.

The fourth objective of this study was to evaluate the growth and condition of smb to help determine if the ecological disturbances in the Great Lakes have caused resource limitations for smb. For example, if the invasions of exotic species had reduced food resources available to smb, then I would have expected to find a decline in smb growth and condition since the 1970s.

My a priori hypothesis was that the smb fishery had declined due to over harvest by recreational anglers in the 1970s and 1980s. Because angler harvest was considered the primary cause of the supposed decline, I expected that rockbass and brown bullhead abundance had not changed since the 1980s. Before this study, I anticipated that mortality of large smb (>350 mm) would be high due to angler harvest. Furthermore, smb condition and growth would be lower than in the 1970s due to resource limitations created by the invasion of exotic species.

Determining what ultimately caused the suspected decline of the smb fishery in the Beaver Islands was difficult because, according to anglers, the population had declined well before this study was conducted. For example, anecdotal evidence suggested that the decline began at least 10 years before this study. Therefore, direct evidence of cormorant predation on smb was nearly impossible to obtain. Gillingham and Seefelt (2001) estimated that the Beaver Islands supported a breeding colony of about 20,000 birds. By comparison, Lenon (unpublished data) estimated smb abundance at less than 5,000 fish, during the peak of the recreational fishery. Given the disparity in relative abundance of smb and cormorants, my research strategy focused on examining the current smb population to identify potential “survival bottlenecks”.

CHAPTER 2

METHODS

Study Site

This study was conducted in the near-shore waters of the Beaver Island Archipelago in northeastern Lake Michigan, Michigan (Figure 2). The Archipelago is located approximately 25-30 km from both the lower and upper peninsulas of Michigan and includes seven large islands: Beaver (15,130 ha), Garden (1,989 ha), High (1,494 ha), Hog (1,024 ha), and Squaw, Trout, and Whiskey (each <53 ha). The Archipelago also includes three small barren islands (<10 ha) that are important nesting grounds for both gulls (*Larus* spp.) and cormorants.

Although the islands are relatively isolated from the mainland, humans have inhabited the Beaver Archipelago for centuries. Native Americans fished and trapped around the islands extensively until Europeans arrived in the early 1800s (Bogue 2001). Fishing, trapping, and logging supported Mormon and, later, Irish settlements on Beaver Island until the early 1900s (BeaverIsland.net 2003). Approximately 400 permanent residents currently live on Beaver Island. The Islands have supported only primitive settlements until recently, yet tourism has been an important part of the local economy since the late 1800s (BeaverIsland.net 2003). Thousands of tourists, many of whom are recreational boaters from throughout the Great Lakes, visit Beaver Island during each summer.

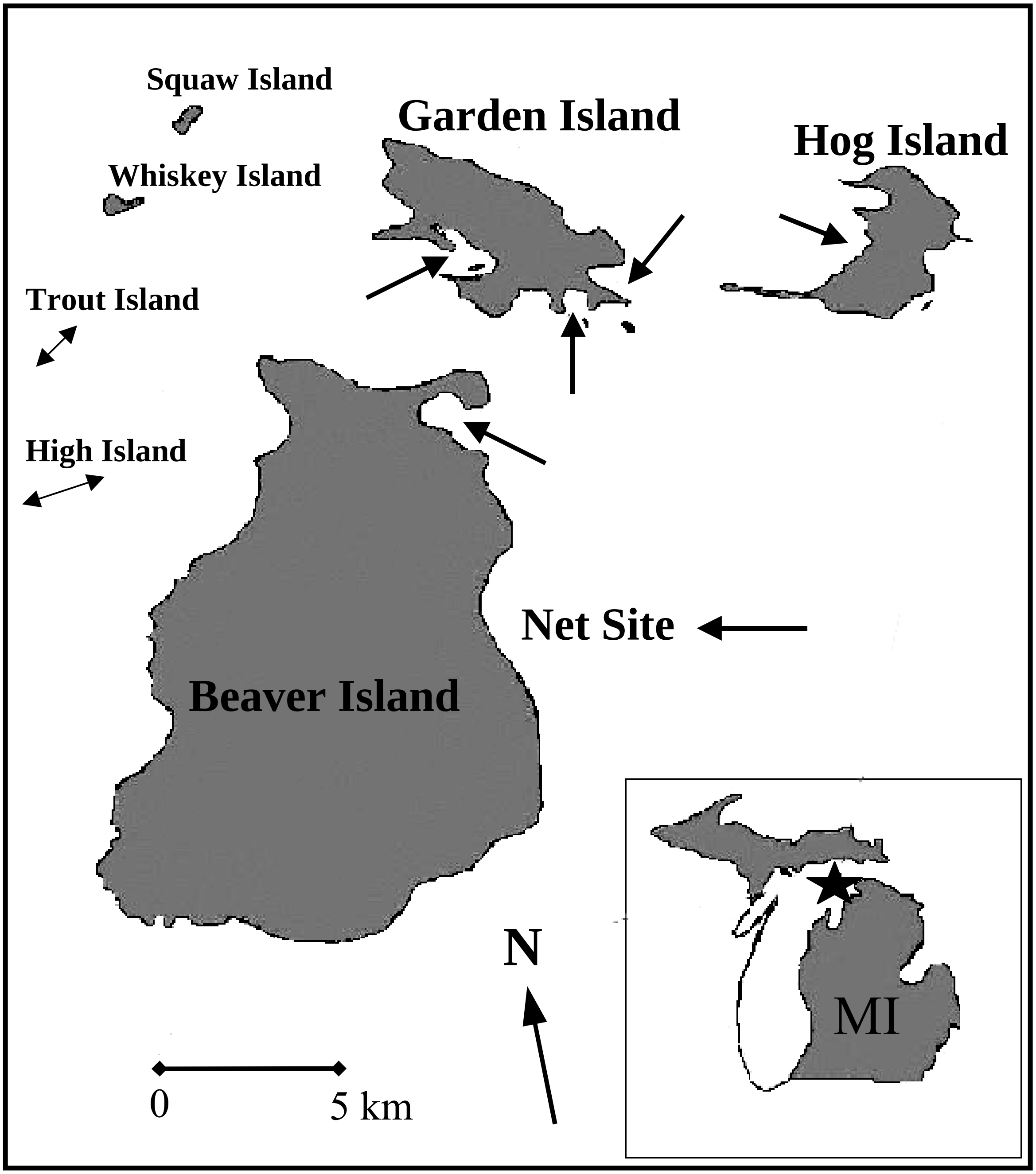

Figure 2. Beaver Island Archipelago, Lake Michigan.

Five bays were chosen for sampling: Garden Island Harbor (GIH), Monatu Bay (MON), Sturgeon Bay (STUR) (all three located on Garden Island), Hog Island Bay (HOG) and St. James Harbor (STJ) (located on Beaver Island) (Figure 2). I focused my effort in the five bays because according to local anglers, these bays historically contained the largest smb populations within the archipelago. In previous years smb populations in GIH, MON, and STJ were sampled to provide baseline data for future work.

The five bays sampled had similar physical features. Typical bottom substrate in the bays was sand, rubble/gravel, and muck. Littoral habitat in each bay contained rock and submerged trees but the habitat in GIH and STUR also had sparse emergent vegetation. The shoreline in the bays was undeveloped except in STJ, where docks and seawalls covered most of the water's edge.

Field Sampling

Smb were sampled with trap nets constructed of 2-cm-square cotton mesh. Each net had two rectangular frames, 1.5 m high by 1.75 m wide, and a pot, 1.5 m high by 1.75 m wide by 2.0 m long, with a 25-m long black cotton lead with 3-cm-square mesh (Figure 3). Trap nets were kept taut in the water by floats (top) and weights (bottom) woven into the mesh. Nets were set 1.25-2.5 m deep and perpendicular to shore. Net sites were chosen by first dividing each bay into blocks of shoreline with suitable depth for netting. Each block was then divided into three potential netting sites. One net site was then chosen randomly from each of these blocks of shoreline (Figure 4). Three to six nets were set throughout each bay (Figure 5-9). Only three nets were used in MON,

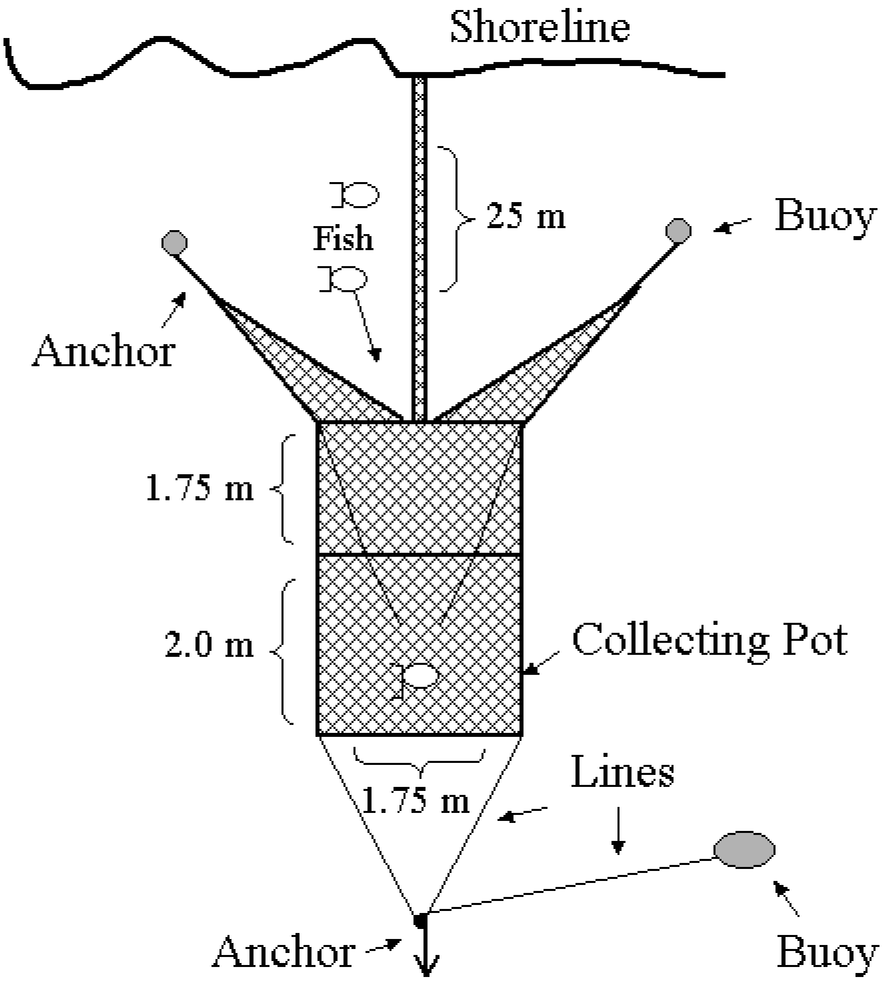

Figure 3. Trap net used for sampling smallmouth bass in the Beaver Archipelago from 1999 through 2002. Not drawn to scale.

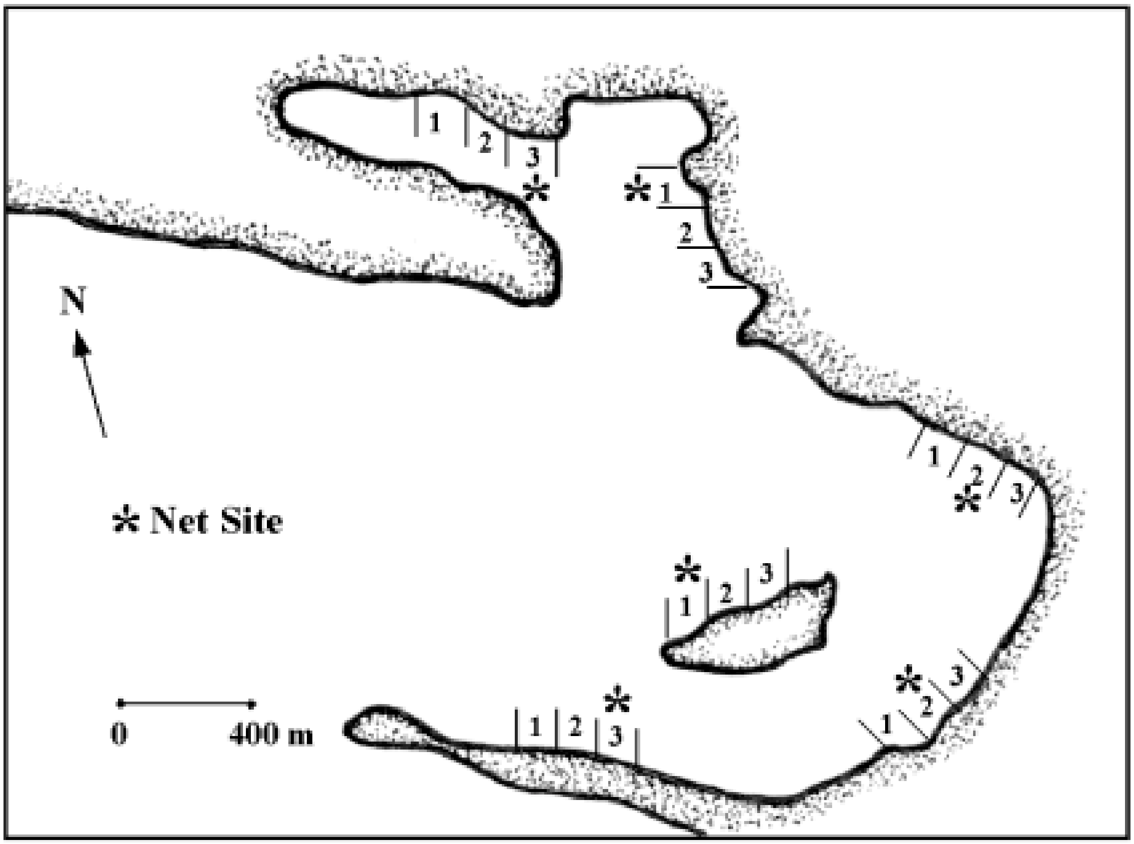

Figure 4. Example of net site selection in Garden Island Harbor from 1999 through 2002. Net sites were randomly chosen from each block of suitable shoreline.

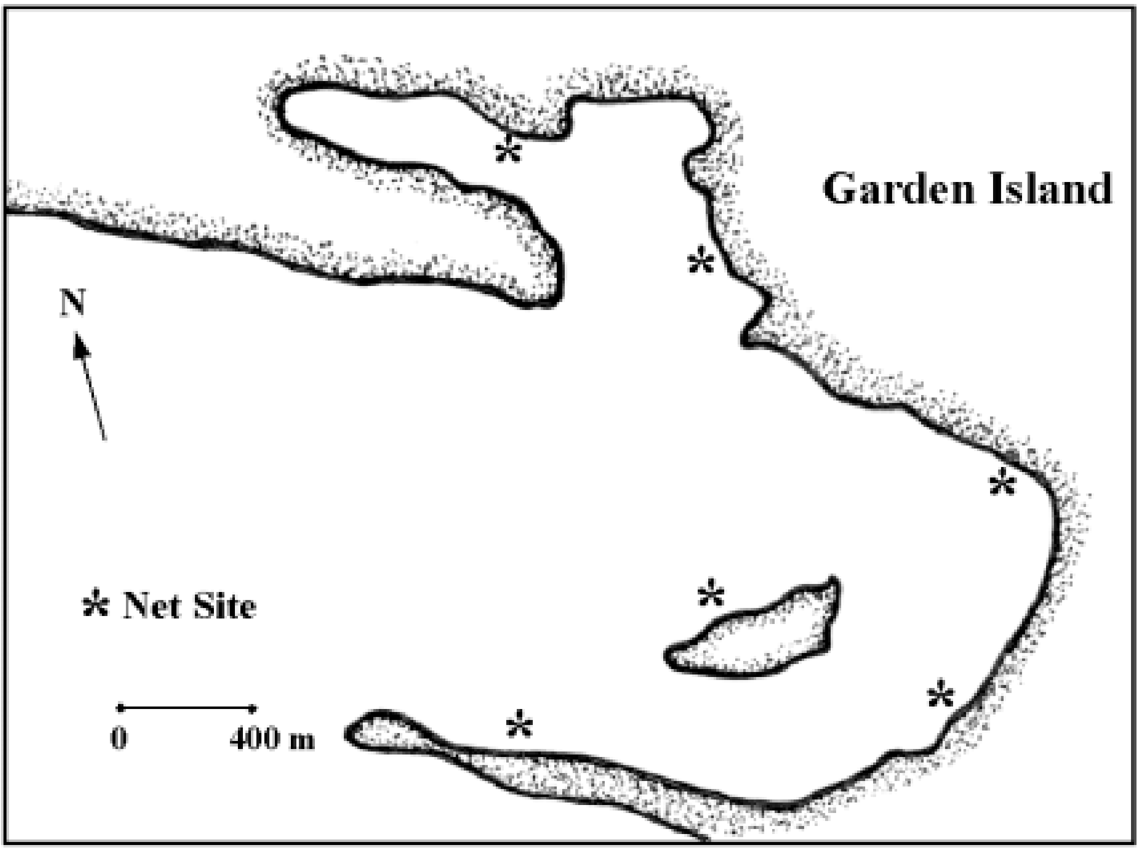

Figure 5. Trap net sites for sampling smallmouth bass in Garden Island Harbor, Garden Island, 1999 through 2002.

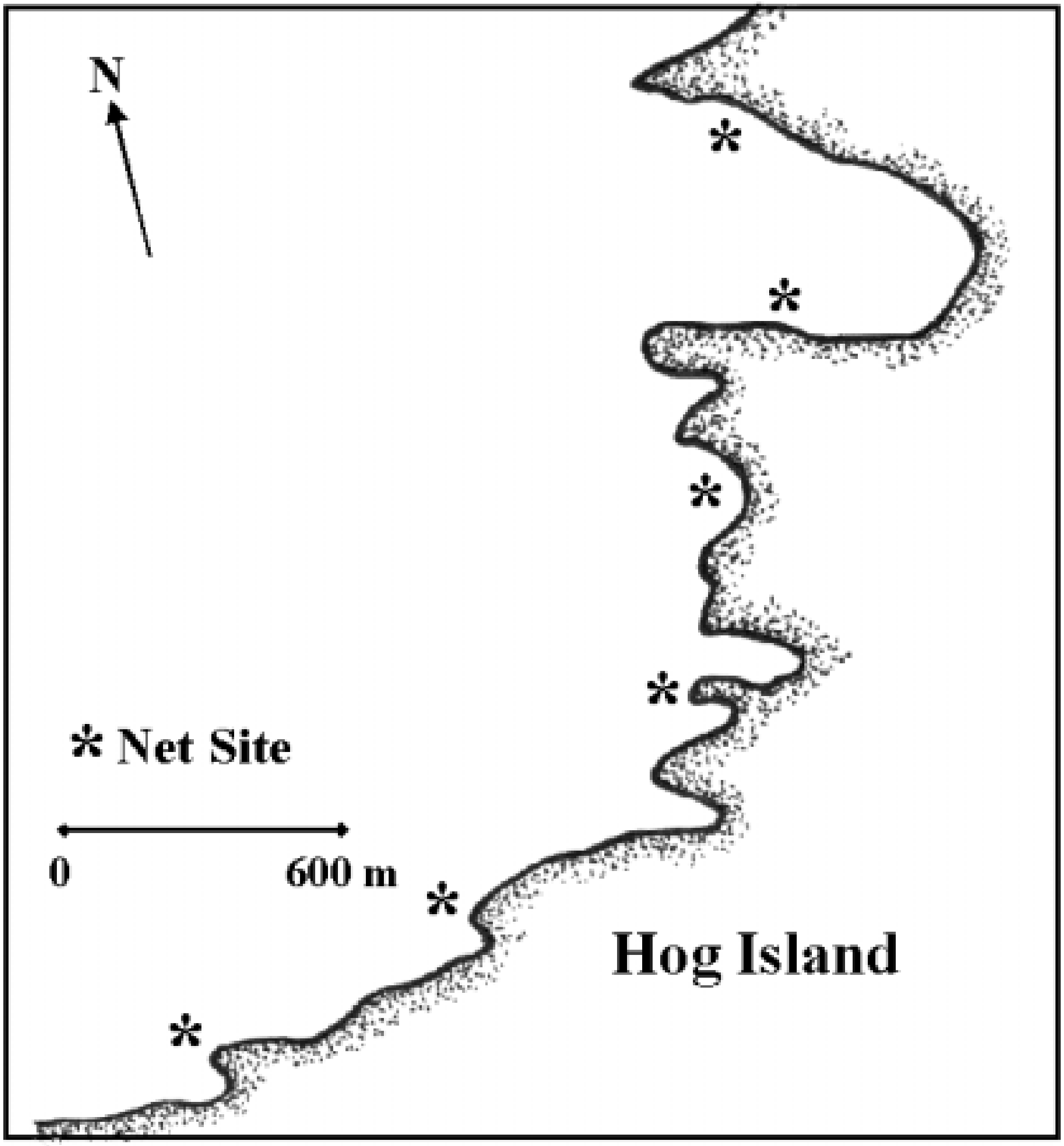

Figure 6. Trap net sites for sampling smallmouth bass along western shoreline of Hog Island, 1999 through 2002.

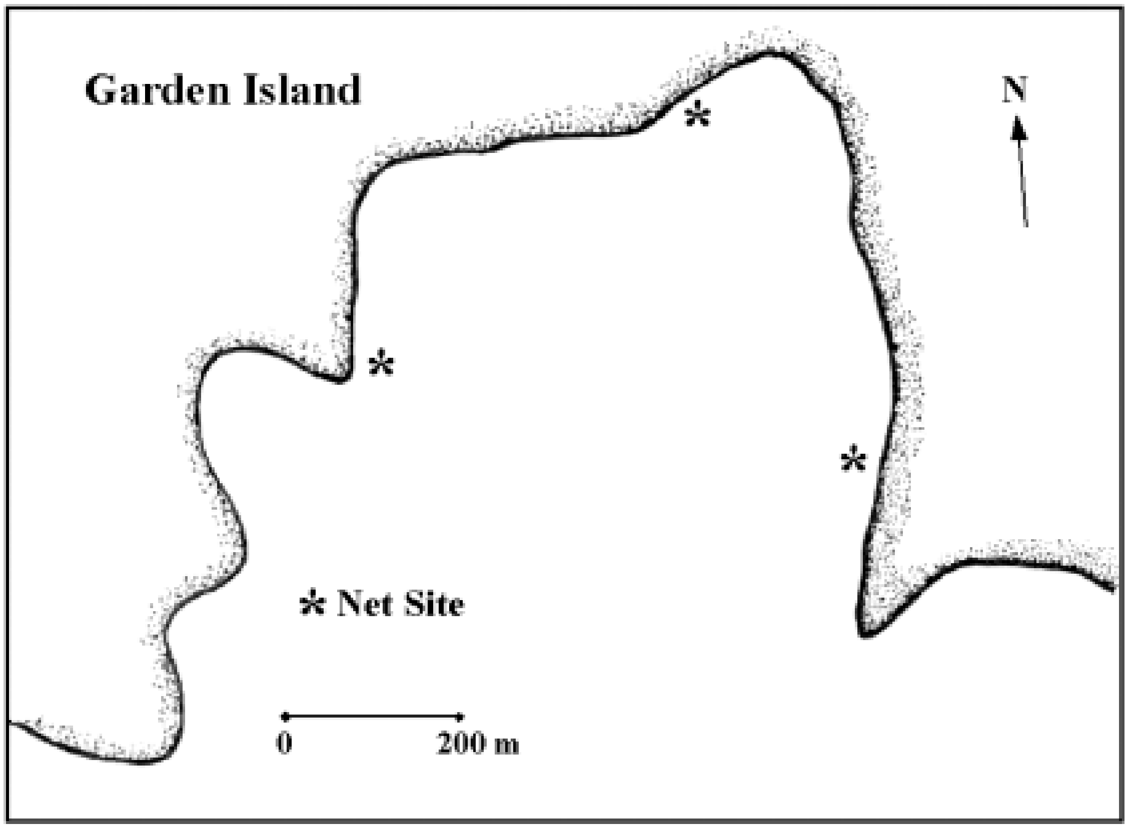

Figure 7. Trap net sites for sampling smallmouth bass in Monatu Bay, Garden Island, 1999 through 2002.

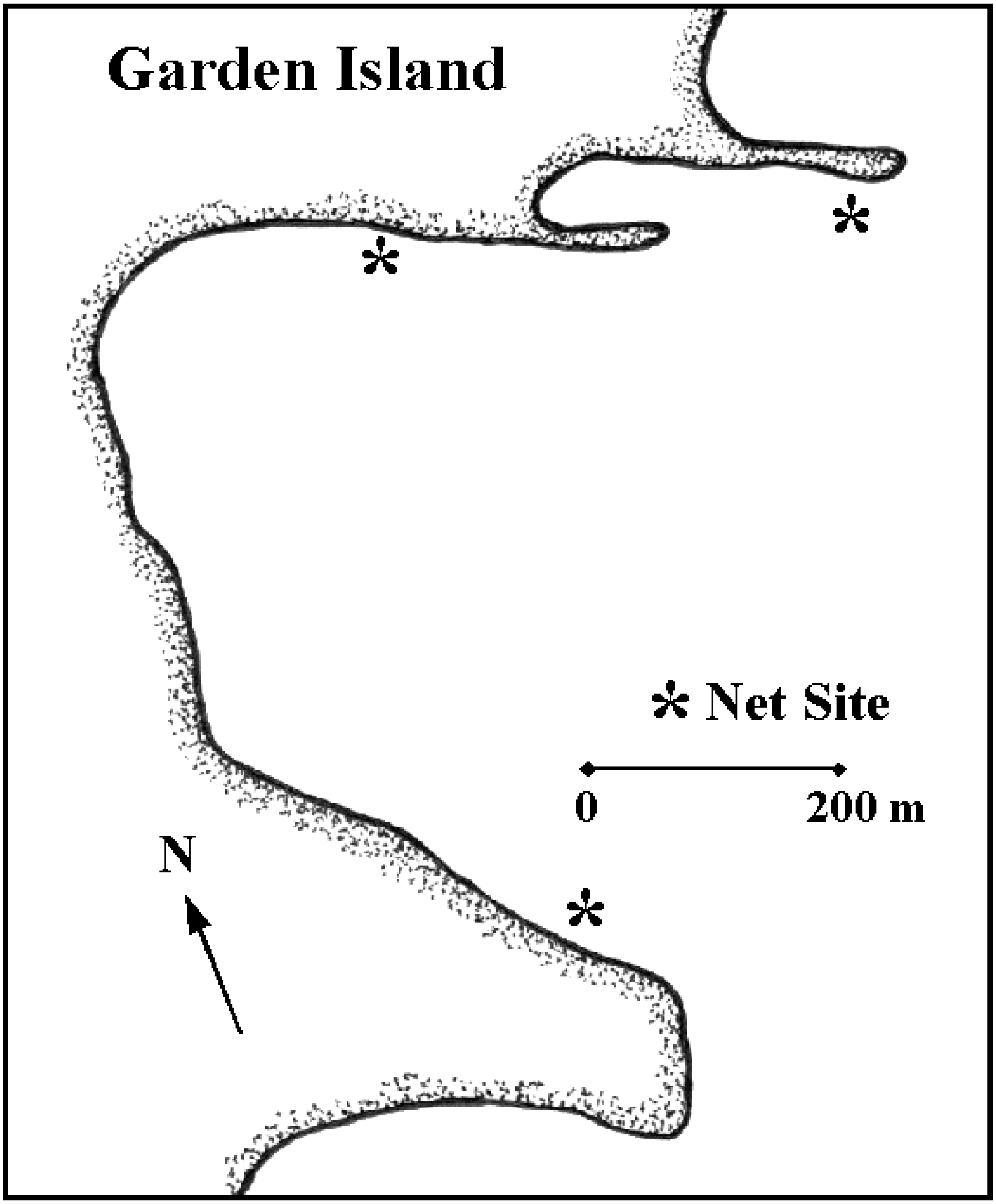

Figure 8. Trap net sites for sampling smallmouth bass in Sturgeon Bay, Garden Island, 1999 through 2002.

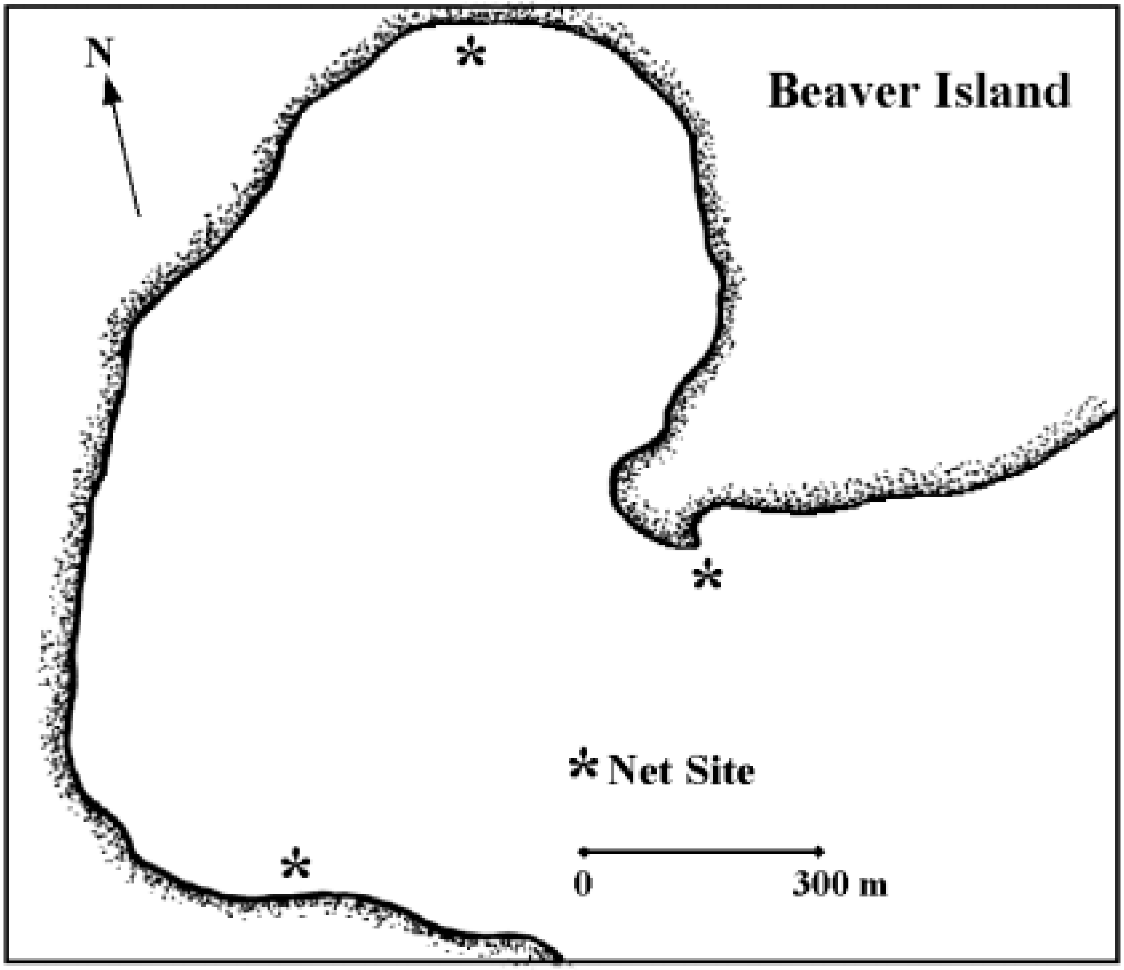

Figure 9. Trap net sites for sampling smallmouth bass in St. James Harbor, Beaver Island, 1999 through 2002.

STUR, and STJ because these bays were relatively small (less suitable netting habitat) and could be sampled thoroughly with fewer nets.

Once set, trap nets were fished for 24 hr periods and checked daily for 7-14 consecutive days. The exact period of sampling in each bay depended on the cumulative number of recaptures obtained. Preliminary data from 1999 indicated that once recapture rates reached 40-50% within a bay, the increase in precision of the estimates resulting from additional recaptures was minimal. Therefore, bays were sampled until the number of recaptures exceeded 40% of the total number of smb marked in that bay.

The bays were sampled sequentially from late May to mid-August in 1999 through 2002 (Table 1). MON and STUR were sampled concurrently because they were relatively smaller bays and could be thoroughly sampled with fewer nets. Unlike the other bays, GIH was sampled twice during the summer in May and then again in July. Sampling in GIH during May was consistent with the other bays; however, it was only used to monitor when smb had fully migrated into shallow water habitat.

When the trap nets were checked, the total length and weight of each smb, rock bass, and brown bullhead captured were recorded. Each smb, rockbass and brown bullhead greater than 150 mm was marked with a uniquely numbered T-bar tag, inserted into the dorsal musculature. Each individual less than 150 mm was marked with an upper caudal (tail) fin clip because small fish can be killed by T-bar tagging. In addition, 3-5 scales from each smb were removed from the dorsal region above the lateral line, between the spiny and soft dorsal fins, for later age determination.

Table 1. Dates on which smallmouth bass were sampled from five bays in the Beaver Archipelgo from 1999 through 2002.

Bay	1999	2000	2001	2002
Garden Island Harbor (1)	05/25-06/09	05/23-06/11	06/04-06/22	06/05-06/18
Garden Island Harbor (2)	07/27-08/08	07/20-08/03	07/24-08/07	07/17-07/31
West Side of Hog Island	06/17-07/01	06/17-06/29	06/26-07/11	06/22-07/03
Monatu Bay	07/14-07/17	07/06-07/18	07/14-07/23	07/07-07/16
Sturgeon Bay	07/04-07/17	07/06-07/18	07/14-07/23	07/07-07/16
St. James Harbor	08/09-08/18	08/08-08/15	08/03-08/09	08/01-08/08

Age Estimation

Ages of the smb were estimated using scales collected from 1999 through 2002. In the lab, the scales were cleaned with water and viewed with a microprojector equipped with a 10-mm lens. Smb age was estimated by counting the annuli formed by the seasonal changes in growth due to water temperatures. To increase the efficiency of this procedure, length-frequency histograms from the total catch from each year were used to estimate the age groups. The number of individuals captured was plotted as a function of fish length and each peak was assigned an age (the assumption is that fish length within each age group is unimodally distributed around the peak value; Devries and Frie 1996). Scales from smb that fell between the peaks in the length-frequency distribution were then analyzed to determine age. Because fish growth in length is greatly reduced after sexual maturity, the variation among individuals within the age groups tends to increase with older fish (Devries and Frie 1996). Therefore, scales were read from all individuals greater than 350 mm.

Population Estimates

Initially, population estimates were calculated with the Schnabel (Schnabel 1938) and Jolly-Seber (Jolly 1965; Seber 1965) models, and with software programs MARK and CAPTURE (Cooch and White 2001). Historical data collected by Lenon (unpublished data), in GIH, MON, and STJ contained only Schnabel population estimates. The Schnabel model, therefore, was the primary estimator used to evaluate changes in smb abundance. The Schnabel estimator is a multiple sample, closed population model designed for concurrent marking and recapturing during a relatively short time period (Krebs 1999). It is best used when the proportion of recaptures in a single recapture period is low (Ricker 1975). To test the assumptions of the Schnabel model, the proportion of marked fish in the catch was plotted against the total number of marked fish (Krebs 1999). A significant ($p < 0.05$) linear relationship (as determined by simple linear regression) indicated that the assumptions were not significantly violated.

The major limitation of the Schnabel model is that it assumes a closed population (Schnabel 1938), which was difficult to test in this study. To test if the data might be better suited for an open population model, the Jolly-Seber estimator also was used to estimate smb abundance (Jolly 1965; Seber 1965). Although Jolly-Seber estimates can be obtained by using program MARK, I calculated the estimates "by hand" within a spreadsheet. The Jolly-Seber estimates however, had wide confidence intervals and were highly variable during the short sampling period probably because of unequal catchability and low recaptures (Krebs 1999). Because of the high estimation uncertainty, the data were probably not suited for the Jolly-Seber model and the estimates were not used for this study.

Another important assumption of the Schnabel model is that of equal catchability (q, the probability of catching an individual fish in one unit of effort) during the sample period, which may be untrue for many fish populations. In most population studies, catchability may vary by sex, age, spatial distribution of animals and sampling effort (Lancia et al. 1994). Unequal catchability also may be caused by individuals that are either caught more often (trap happy) or caught less often (trap shy) than the rest of the population. The more severe the violation of equal catchability, the more biased the estimate (Schnabel 1938). To test the assumption of equal catchability, smb abundance was estimated with the closed capture option within the programs MARK and

CAPTURE, which choose estimation models that fit the variability in catchability. The Schnabel model is one of the potential models within CAPTURE; thus, if the assumption of equal catchability during the sampling period were met, then the Schnabel model would be chosen as the most appropriate by CAPTURE.

Preliminary analyses indicated that the data were not suited for MARK. Low capture probabilities, due to a low frequency of repeated recaptures, apparently caused MARK to produce population estimates with unrealistically low standard error (M. Conroy, University of Georgia, pers. comm.). For example, GIH was estimated to have 241 smb in 1999, with lower and upper confidence intervals of 241 and 241. MARK apparently used the number of fish captured during the sampling period (241) as the estimate of population size. This problem existed for all bays in all years; therefore, the estimates obtained from MARK were considered invalid.

Although MARK was not effective for my data, population estimates were calculated using the most appropriate model of catchability from CAPTURE (Cooch and White 2001). Program CAPTURE examines the encounter history of each fish, and then chooses a model that “best” suits the variability in catchability (Lancia 1994). CAPTURE chooses from the following models: M_0, where catchability is equal for the population, M_h, where each fish has a unique capture probability that remains constant during the sample period, M_b, which allows a change in capture probabilities caused by a response to trapping, M_t, where each fish is assumed to have equal catchability during the sample period (Schnabel method), and M_{bh}, M_{th}, M_{tb}, M_{tbh}, which are combinations of these previous models (Lancia et al 1994). The most appropriate model is determined by CAPTURE based on goodness-of-fit tests and tests between models (Lancia et al. 1994).

Using both, the Schnabel estimator and the most appropriate model of catchability chosen by program CAPTURE (which may be the Schnabel model) (hereafter: CAPTURE model), population estimates for smb, rockbass, and brown bullhead were calculated for each bay from 1999 to 2002. Rockbass and brown bullhead abundance was estimated only using the Schnabel estimator because the recapture rate was too low for CAPTURE. Rockbass and brown bullhead abundances also were only estimated in GIH because the populations of these species were too small to be estimated in the other four bays. Cumulative population estimates for smb were not attempted because the capture probability models from CAPTURE differed among bays and years sampled (Table 2).

Catch-Per-Unit-Effort

Catch-per-unit-effort (CPUE) was calculated for smb as a secondary method of evaluating abundance trends. Effort was defined as a net-night, which equaled one net set for approximately 24 hr. Catch-per-unit effort is a measure of relative abundance that can be used to make temporal or spatial comparisons (Ney 1999). To make valid comparisons with CPUE, sampling effort must be standardized. Use of relative abundance relies on the assumption that CPUE is directly proportional to population size (Ney 1999), however, this assumption requires that catchability remains constant among all samples. Catchability however, rarely remains constant due to changes in fish activity patterns, weather, and water quality (Ney 1999). Because sampling in this study was standardized and conducted over a period of 10-14 days, the effects of short-term changes in catchability were probably minimized. To test for significant ($\alpha = 0.05$) changes in

Table 2. Most appropriate model of smallmouth bass catchability chosen by program CAPTURE for the five bays sampled in the Beaver Archipelago, 1999 through 2002.

	Sample Site				
Year	Garden Island Harbor	Hog Island	Monatu Bay	Sturgeon Bay	St. James Harbor
1999	Choa's M(th)	Choa's M(th)	M(tbh)	Darroch M(t)	Chao's M(th)
2000	Burnham's M(tb)	Burnham's M(tb)	Choa's M(th)	Darroch M(t)	Darroch M(t)
2001	Choa's M(th)	Darroch M(t)	M(tbh)	Choa's M(th)	Zippin M(b)
2002	Darroch M(t)	Burnham's M(tb)	Choa's M(th)	Choa's M(th)	Darroch M(t)

smb CPUE among years within each bay, a nested, mixed ANOVA was used with sampling date and net site (random effects) nested within year (fixed effect). Tukey's multiple comparison procedure was used when CPUE was significantly different among years.

Age-Specific Mortality Rates

Annual change in smb cohort size within each bay was used to determine age-specific mortality rates in each sequential year of this study. Smallmouth bass cohort size for ages 3-13 was estimated using both the Schnabel and CAPTURE models. Cohort size for ages 1 and 2 was not calculated because smb at these ages were not fully susceptible to the trap nets as evidenced by the lower abundance of age 1 and 2 than age 3 in the length frequency histograms. Smallmouth bass age 1 and 2 also were rarely captured during sampling, indicating that fish recruited to the gear at some point during their third year of life. Data from ages 8-13 were combined because sample size was low and the accuracy of age estimation decreases with larger fish (Devries and Frie 1996). Raw catch data were combined from all bays (length-frequency histograms) to further evaluate trends in annual mortality rates.

Condition Factor

Smallmouth bass condition in 2002 was evaluated using relative weights, a method that compares a hypothetical standard weight-at-lengths to actual values from the population in question (Wege and Anderson 1978; Kolander et al. 1993). The hypothetical standard weight-at-lengths are calculated using a weight-length equation based on a species-specific slope and intercept value (Kolander et al. 1993). In theory, a mean relative weight of 100 for a range of size groups may indicate ecological and physiological optimality for a population (Van Den Avyle and Hayward 1999). Because there is contention regarding the use of relative weight as a measure of optimality for individual fish, I evaluated general trends in smb condition (simple linear regression for length and relative weight). A significant ($\alpha = 0.05$) relationship (positive or negative) between length and relative weight would indicate a potential length-specific resource limitation. A one-way ANOVA was used to test if relative weights were significantly different among the bays sampled during this study (Dowdy and Weardon 1985). The five bays served as the treatments and relative weight was assigned as the response variable. Tukey's multiple comparison procedure was used to determine which treatment means were significantly ($\alpha = 0.05$) different.

Growth

Smallmouth bass growth was analyzed by determining mean length-at-age in 2001. Mean length-at-age from 2001 were used for this study because sample size was larger, thus precision was better. To further increase sample size, catch data from the five bays were combined. Actual mean length-at-age was compared to predicted values from a von Bertalanffy growth equation (von Bertalanffy 1938). The von Bertalanffy growth equation was used to qualitatively evaluate growth of smb from the Beaver Archipelago. For example, if the actual mean length for smb age-3 was less than the predicted value, then that cohort grew slower than expected for that particular population. To evaluate potential changes in growth over the last three decades, a paired t-test was used to test the difference in length-at-ages from 1972 and 2001 (Dowdy and Weardon 1985). Analyses were conducted with $\alpha = 0.05$.

CHAPTER 3

RESULTS

Total Catch Data of Smallmouth Bass

From May 1999 to August 2002, 3,167 smb were captured in the Beaver Archipelago (Table 3) in 917 net/nights. Total captures declined from 1999 through 2001 then increased in 2002, but total CPUE did not change significantly ($F_{3, 656} = 0.96$, $p = 0.330$) during this study. The total number of captures included marked and unmarked individuals for each day. Because smb were recaptured on multiple occasions, the number of individuals that were marked was less than the number of captures in each year. The proportion of marked individuals that were recaptured was greater than 60% in each year.

Table 3. Total catch statistics and catch-per-unit-effort (CPUE; fish/net night; 95% confidence intervals) of smallmouth bass in the Beaver Archipelago from 1999 through 2002. CPUE followed by the same lowercase letter are not significantly different ($\alpha = 0.05$) based on Tukey's post hoc test.

Year	Total captures[1]	Catch-per-unit-effort	Total marked	Total recaptures
1999	1202	4.6^a (3.2-5.9)	632	516
2000	712	4.4^a (3.8-5.1)	418	248
2001	599	3.3^a (1.9-4.6)	359	227
2002	654	3.9^a (2.5-5.3)	386	244

[1] Total captures included marked and unmarked fish from each sample occasion.

Total length of smb captured in the Beaver Archipelago from 1999 through 2002 ranged from 110 mm to 530 mm (Figure 10). Although a relatively large number of smb less than 300 mm (278-770 individuals) were captured each year, the individuals from 300-400 mm in total length were 67-80% less abundant. In fact, larger smb (>400 mm) were actually more common than were individuals between 300-400 mm.

Garden Island Harbor

In GIH, the number of smb that were captured, marked and recaptured declined from 1999 to 2001 but increased in 2002 (Table 4). From 1999 through 2002, CPUE varied from 1.4-5.5 smb per net night and was significantly different among years ($F_{3,\ 250} = 13.29$, $p < 0.0001$). Tukey's multiple comparison procedure indicated that CPUE in 1999 was greater than in 2001 and 2002.

Table 4. Catch statistics, catch-per-unit-effort (CPUE; fish/net night; 95% confidence intervals) and population estimates (95% confidence intervals) of smallmouth bass in Garden Island Harbor, 1999 through 2002. CPUE followed by the same lowercase letter are not significantly different ($\alpha = 0.05$) based on Tukey's post hoc test.

Year	Total captures[1]	Catch-per-unit-effort	Total marked	Total recaptures	Schnabel (N)	CAPTURE (N)
1999	473	5.5[a]	224	241	237	366
		(4.6-6.4)			(210-271)	(323-433)
2000	158	3.4[ab]	80	73	104	79
		(2.2-4.6)			(85-135)	(76-95)
2001	122	1.4[b]	79	42	127	106
		(0.5-2.3)			(110-150)	(92-135)
2002	236	3.1[b]	146	84	221	186
		(2.1-4.1)			(182-281)	(165-219)

[1] Total captures included both marked and unmarked individuals.

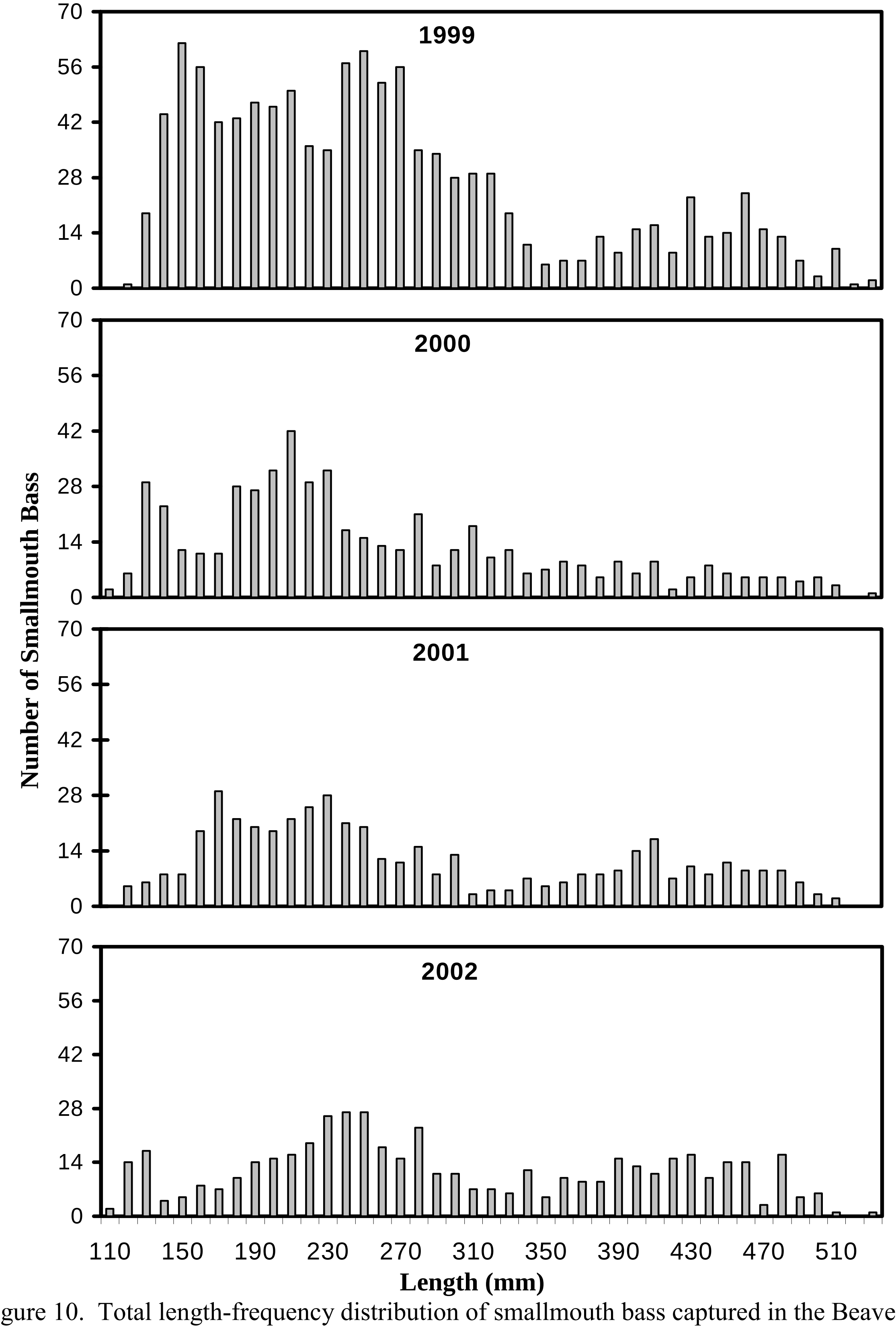

Figure 10. Total length-frequency distribution of smallmouth bass captured in the Beaver Archipelago.

In GIH, population estimates of smb from the Schnabel model and program CAPTURE (most appropriate model of catchability for each year) ranged from 79 to 366 from 1999 through 2002 (Table 4). Although the confidence intervals were usually wider for the Schnabel estimates, the population estimates obtained from the Schnabel and CAPTURE models were similar from 1999 through 2002 (Table 4). Furthermore, Schnabel population estimates from 1999 through 2002 were 85-95% lower than in the 1970s and 1980s (Figure 11).

CAPTURE indicated that the Schnabel model (M_t) was most appropriate only in 2002 (Table 2). The assumption of equal catchability of smb during the sample period, therefore, was violated in 1999, 2000, and 2001. A linear relationship ($p < 0.05$) also was found between the number of marked individuals and the proportion of marked individuals in the catch (assumptions were met) for the Schnabel population estimates in 2000 and 2001 (Figure 12).

Cohort estimates of smb from the Schnabel and CAPTURE models were similar within each year from 1999 through 2002 in GIH (Table 5). Schnabel estimates generally had wider confidence intervals than the estimates from the CAPTURE models. Annual mortality rates for smb ages 3-6 and 8-13, from both estimators, ranged from -2.33 to 0.97 and –1.00 to 0.79, respectively (Table 6). A negative mortality rate indicated that the cohort estimate had increased from the previous year. Annual mortality for ages 3 and 4 between 1999-2000 and 2000-2001 was 2-3 times higher than for older cohorts.

During 2002, 208 smb were measured in GIH, ranging from 20 g at 115 mm to 2450 g at 480 mm. Relative weights ranged from 65 at 190 mm to 195 at 135 mm, with a mean of 129 (S.D. = 19) (Figure 13). Mean relative weight was significantly different

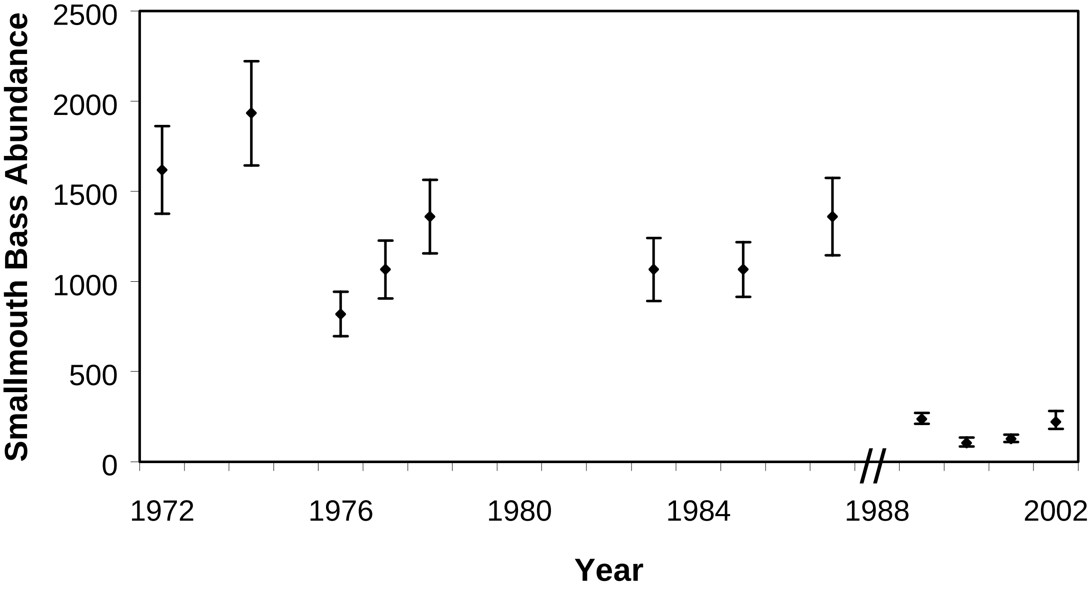

Figure 11. Schnabel population estimates (95% confidence intervals) of smallmouth bass in Garden Island Harbor, 1972 through 2002. Estimates for 1972 through 1987 from Lenon (unpublished data).

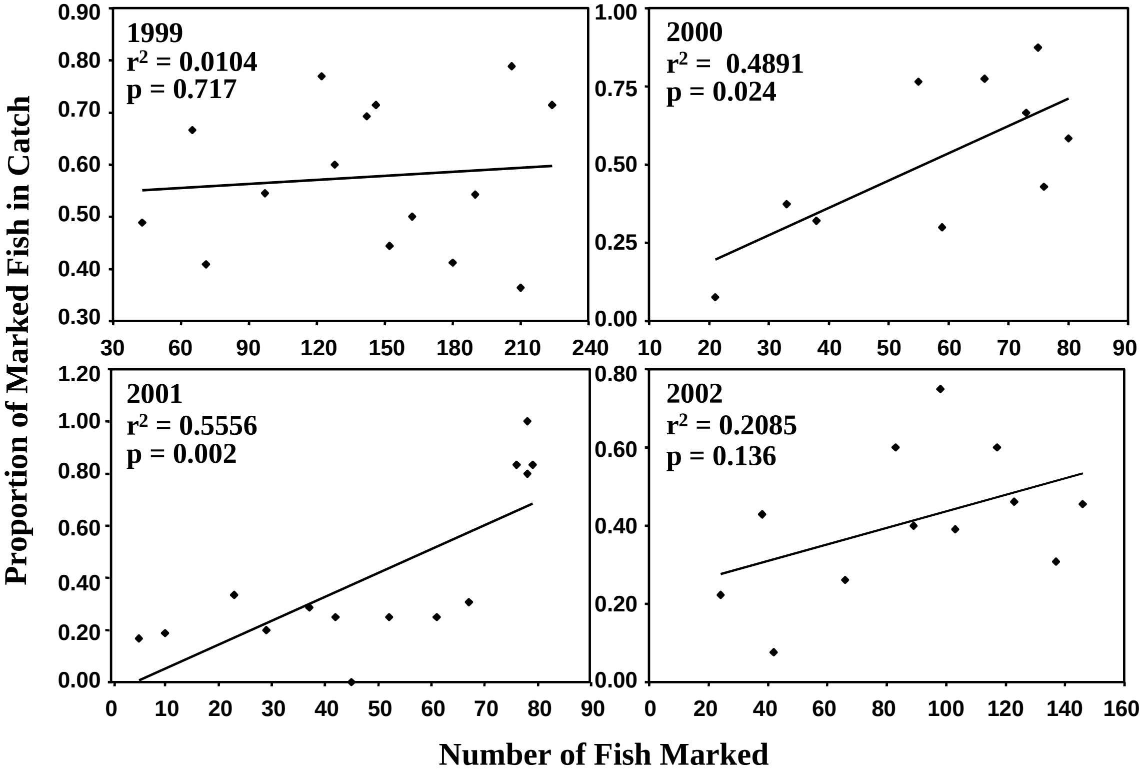

Figure 12. Regression analyses of smallmouth bass capture data from Garden Island Harbor, 1999 through 2002. A linear relationship ($p < 0.05$) indicated that the assumptions of the Schnabel population estimator were met during sampling.

Table 5. Estimates of cohort abundance (95% confidence intervals) of smallmouth bass in Garden Island Harbor, 1999 through 2002. Cohort abundance of age 1 and 2 was not estimated and ages 8 through 13 were combined.

	Schnabel Model				CAPTURE Model			
Age	1999	2000	2001	2002	1999	2000	2001	2002
3	99 (76-143)	50 (32-97)	25 (15-47)	82 (44-174)	102 (88-128)	32 (31-33)	31 (26-51)	139 (98-209)
4	73 (60-93)	20 (12-38)	15 (8-36)	53 (38-85)	114 (87-317)	16 (15-17)	16 (14-30)	59 (48-91)
5	19 (13-32)	5 (2-14)	6 (1-60)	16 (9-16)	21 (20-22)	3 (2-5)	2 (1-22)	15 (13-30)
6	5 (1-45)	3 (1-30)	9 (2-90)	3 (1-20)	6 (5-17)	2 (1-21)	3 (2-4)	4 (3-12)
7	5 (3-11)	7 (4-16)	10 (5-25)	7 (2-70)	8 (8-14)	5 (4-7)	11 (10-21)	5 (4-21)
8-13	29 (13-80)	20 (9-31)	15 (3-31)	30 (18-53)	83 (52-149)	17 (15-91)	11 (10-12)	18 (12-19)

Table 6. Annual age-specific mortality rates (95% confidence intervals) of smallmouth bass in Garden Island Harbor, 1999 through 2002. Cohort abundance of age 1 and 2 was not estimated and ages 8 through 13 were combined.

	Schnabel Model			CAPTURE Model		
Age	1999-2000	2000-2001	2001-2002	1999-2000	2000-2001	2001-2002
3	0.79 (0.50-0.92)	0.70 (-0.12-0.92)	-1.12 (-4.66-0.19)	0.84 (0.82-0.88)	0.50 (0.00-0.56)	-0.90 (-2.50-0.06)
4	0.93 (0.77-0.98)	0.70 (-0.12-0.92)	-0.07 (-3.12-0.75)	0.97 (0.94-0.99)	0.88 (-0.46-0.94)	0.06 (-1.14-0.57)
5	0.84 (-1.31-0.97)	-0.80 (-4.40-0.86)	0.50 (-1.90-0.98)	0.90 (-0.40-0.76)	0.00 (-0.50-0.60)	-1.00 (-1.10-0.86)
6	-0.40 (-1.50-0.91)	-2.33 (-2.44-0.83)	0.22 (-3.40-0.98)	0.17 (-0.40-0.07)	-4.50 (-2.00-0.52)	-0.64 (-9.50-0.33)
8-13	0.31 (-1.38-0.89)	0.25 (-2.44-0.90)	-1.00 (-1.60-0.42)	0.79 (-0.75-0.90)	0.35 (0.26-0.89)	-0.63 (-0.80-0.00)

among the bays ($F_{4, 455} = 41.76$, $p < 0.0001$). Tukey's post hoc test indicated that mean relative weight of smb from GIH was higher than that of HOG. Six smb had relative weights lower than 100, however all of these fish were less than 250 mm suggesting that weighing errors of small fish were probably responsible. Relative weight in GIH, however, was not significantly correlated with total length ($R^2 = 0.0341$, $p = 0.007$).

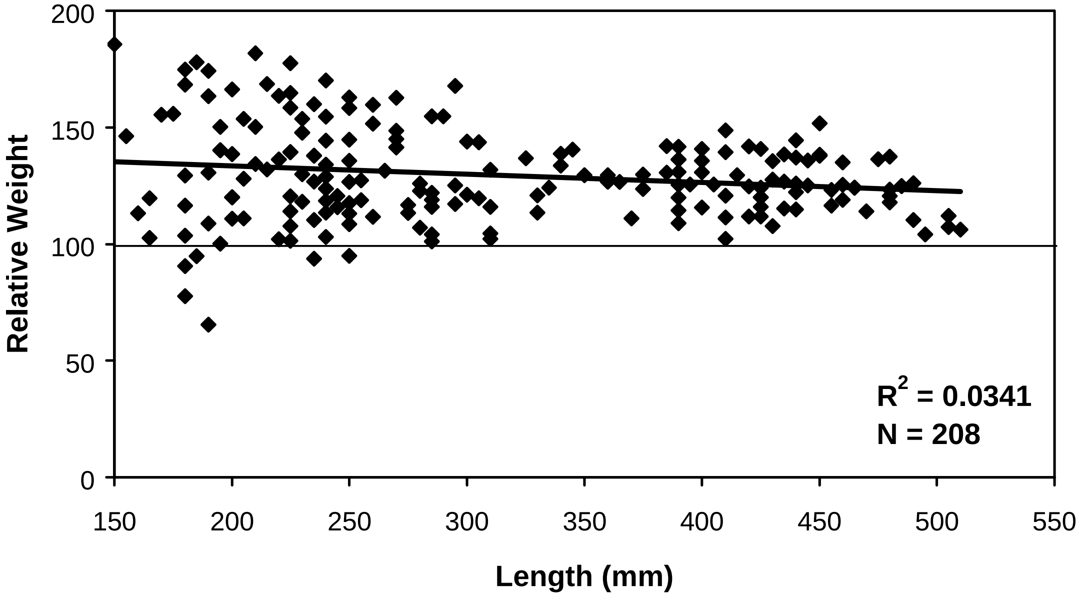

Figure 13. Relative weights of smallmouth bass captured in Garden Island Harbor in 2002. Relative weight of 100 indicates individual was at expected weight-at-length.

The total number of rockbass captured in GIH declined from 1999 to 2002 (Table 7). In 2002, the number of recaptures exceeded the number of rockbass marked because individuals were recaptured on multiple occasions. The number of brown bullhead captured in GIH increased from 1999 to 2000 but then declined sharply from 2000 to 2002 (Table 8). In 2000 and 2001, the number of recaptures was greater than the number of brown bullhead marked because individuals were recaptured on several occasions.

Table 7. Catch statistics and Schnabel population estimates (95% confidence intervals) of rockbass in Garden Island Harbor, 1984 and 1999 through 2002. Population estimate for 1984 from Lenon (unpublished data).

Year	Total captures[1]	Total marked	Total recaptures	Population estimate
1984	N/A	N/A	N/A	3113 (2035-4882)
1999	71	59	11	185 (103-376)
2000	65	40	22	64 (42-102)
2001	65	48	40	48 (38-59)
2002	24	8	16	8 (5-14)

[1] Total captures included both marked and unmarked individuals.

Table 8. Catch statistics and Schnabel population estimates (95% confidence intervals) of brown bullhead in Garden Island Harbor, 1984 and 1999 through 2002. Population estimate for 1984 from Lenon (unpublished data).

Year	Total captures[1]	Total marked	Total recaptures	Population estimate
1984	N/A	N/A	N/A	6538 (5055-8446)
1999	36	26	10	41 (22-87)
2000	82	27	54	27 (21-35)
2001	23	11	12	11 (6-22)
2002	6	4	1	4 (1-6)

[1] Total captures included both marked and unmarked individuals.

Schnabel population estimates of rockbass and brown bullhead both decreased 72-98% from 1999 through 2002 (Table 7 and 8). Population estimates of both species also had declined 99% since 1984 (Table 7 and 8).

Western Hog Island

At HOG, the number of smb that were captured, marked and recaptured declined each year from 1999 through 2002 (Table 9). From 1999 through 2002, CPUE varied from 2.4-5.5 smb per net night and was significantly different among years ($F_{3,\,235} = 12.03$, $p < 0.0001$; Table 9).

Table 9. Catch statistics, catch-per-unit-effort (CPUE; fish/net night; 95% confidence intervals), and population estimates (95% confidence intervals) of smallmouth bass along the western shoreline of Hog Island, 1999 through 2002. CPUE followed by the same lowercase letter are not significantly different ($\alpha = 0.05$) based on Tukey's post hoc test.

Year	Total captures[1]	Catch-per-unit-effort	Total marked	Total recaptures	Schnabel (N)	CAPTURE (N)
1999	457	5.5[a]	233	186	333	524
		(4.7-6.3)			(293-389)	(447-636)
2000	306	4.9[a]	166	106	211	406
		(4.0-5.9)			(181-254)	(187-792)
2001	189	2.4[b]	119	74	164	157
		(1.5-3.2)			(134-212)	(140-187)
2002	172	2.8[b]	98	71	129	163
		(1.8-3.7)			(105-168)	(109-214)

[1] Total captures included both marked and unmarked individuals.

Population estimates of smb from the Schnabel and CAPTURE models varied from 129 to 524 from 1999 through 2002 (Table 9). Although estimates from the CAPTURE models were higher than Schnabel estimates in 1999 and 2002, they exhibited similar trends from 1999 through 2002 (Table 9).

CAPTURE indicated that the Schnabel catchability model was most appropriate only in 2001 (Table 2), indicating that the assumption of equal smb catchability during the sample period was violated in 1999, 2000, and 2002. The assumptions were met for the Schnabel population estimates in 1999, 2000, and 2001 (Figure 14).

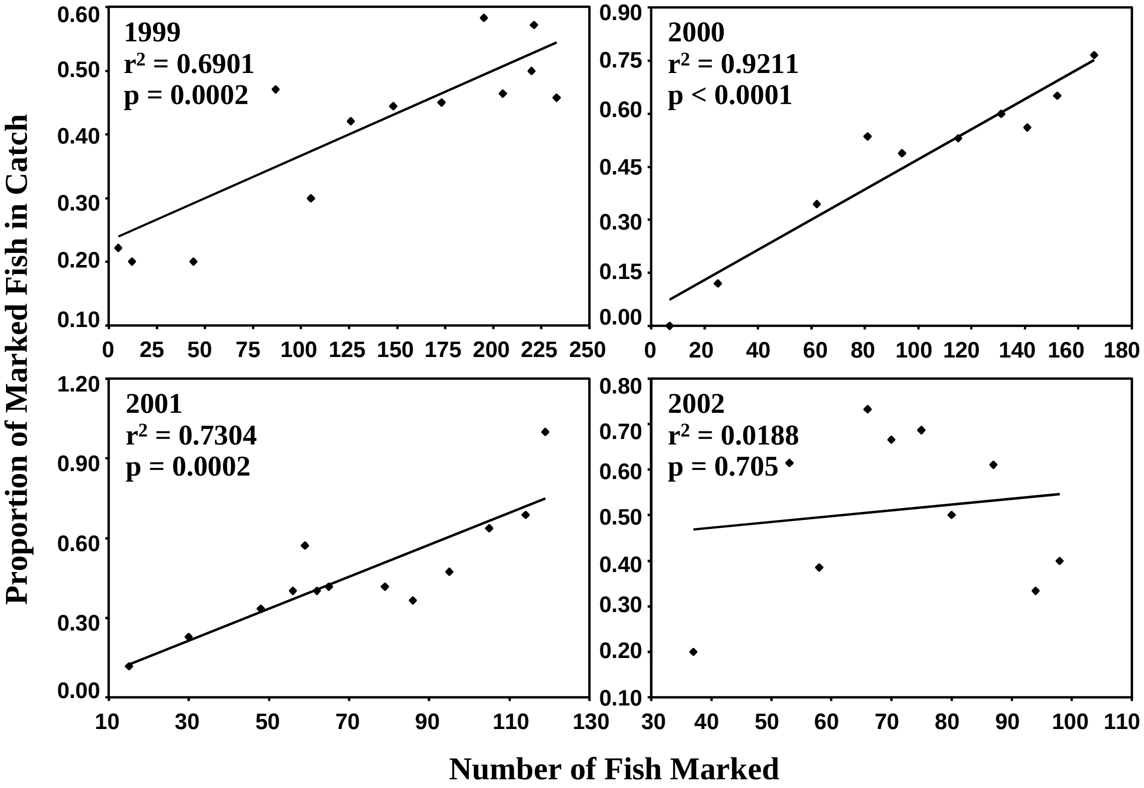

Figure 14. Regression analyses of smallmouth bass capture data from along western Hog Island, 1999 through 2002. A linear relationship ($p < 0.05$) indicated that the assumptions of the Schnabel population estimator were met during sampling.

Cohort estimates of smb from the Schnabel and CAPTURE models from each year were similar (Table 10). Specific age cohorts decreased by as much as 50% between each year from 1999 through 2002. The cohort estimates from HOG, especially for older cohorts, were less precise than those from GIH (wider confidence intervals). Annual mortality rates for smb ages 3-6 and 8-13, from both estimators, ranged from –0.17 to

0.93 and –0.69 to 0.17, respectively (Table 10). Annual mortality for ages 3-5 was 2-3 times higher than for older cohorts from 1999 to 2000 and 2000 to 2001 (Table 11).

Table 10. Estimates of cohort abundance (95% confidence intervals) of smallmouth bass along western Hog Island, 1999 through 2002. Cohort abundance of age 1 and 2 was not estimated and ages 8 through 13 were combined.

	Schnabel Model				Program CAPTURE			
Age	1999	2000	2001	2002	1999	2000	2001	2002
3	316 (197-542)	107 (72-169)	70 (34-176)	42 (16-166)	283 (204-423)	117 (92-162)	61 (42-109)	32 (21-70)
4	80 (64-106)	22 (14-39)	27 (15-54)	97 (17-410)	90 (82-107)	30 (23-53)	21 (19-32)	15 (14-24)
5	64 (49-91)	46 (35-69)	13 (7-30)	13 (6-36)	59 (54-72)	42 (38-54)	17 (14-33)	11 (10-13)
6	14 (9-24)	13 (8-23)	12 (5-46)	20 (8-61)	12 (11-14)	14 (13-20)	38 (22-76)	12 (11-13)
7	4 (2-9)	15 (8-26)	10 (6-17)	11 (6-20)	4 (3-5)	14 (13-21)	12 (11-29)	14 (12-22)
8-13	24 (15-42)	24 (16-39)	26 (16-43)	44 (34-65)	29 (25-45)	24 (21-37)	25 (21-42)	38 (47-54)

Table 11. Annual age-specific mortality rates (95% confidence intervals) of smallmouth bass along western Hog Island, 1999 through 2002. Cohort abundance of age 1 and 2 was not estimated and ages 8 through 13 were combined.

	Schnabel Model			Program CAPTURE		
Age	1999-2000	2000-2001	2001-2002	1999-2000	2000-2001	2001-2002
3	0.93 (0.80-0.97)	0.75 (0.25-0.91)	-0.39 (-1.10-0.90)	0.89 (0.74-0.95)	0.82 (0.65-0.88)	0.75 (0.43-0.87)
4	0.42 (-0.07-0.67)	0.41 (-1.14-0.82)	0.52 (-1.40-0.89)	0.53 (0.34-0.64)	0.43 (-0.43-0.74)	0.48 (0.32-0.69)
5	0.80 (0.53-0.91)	0.74 (-0.31-0.93)	-0.54 (-7.71-0.73)	0.76 (0.63-0.82)	0.09 (-1.00-0.59)	0.29 (0.07-0.67)
6	-0.07 (-1.89-0.67)	0.23 (-1.12-0.74)	0.08 (-3.00-0.87)	-0.17 (-0.75-0.07)	0.14 (-1.20-0.45)	0.63 (0.00-0.84)
8-13	0.00 (-1.60-0.62)	-0.08 (-1.69-0.59)	-0.69 (-3.06-0.21)	0.17 (-0.48-0.53)	-0.04 (-1.00-0.43)	-0.52 (-1.57-0.11)

In 2002, 102 smb were measured in HOG, ranging from 30 g at 125 mm to 2880 g at 490 mm. Relative weights ranged from 97 at 245 mm to 196 at 400 mm, with a mean of 120 (S.D. = 14) (Figure 15). Only one smb had a relative weight less than 100. Mean relative weight was significantly different among the bays ($F_{4, 455} = 41.76$, $p < 0.0001$). A Tukey's post hoc test indicated that mean relative weight of smb from HOG was significantly less than in GIH and STJ. In addition, relative weight was not significantly correlated with total length ($R^2 = 0.0007$, $p = 0.846$).

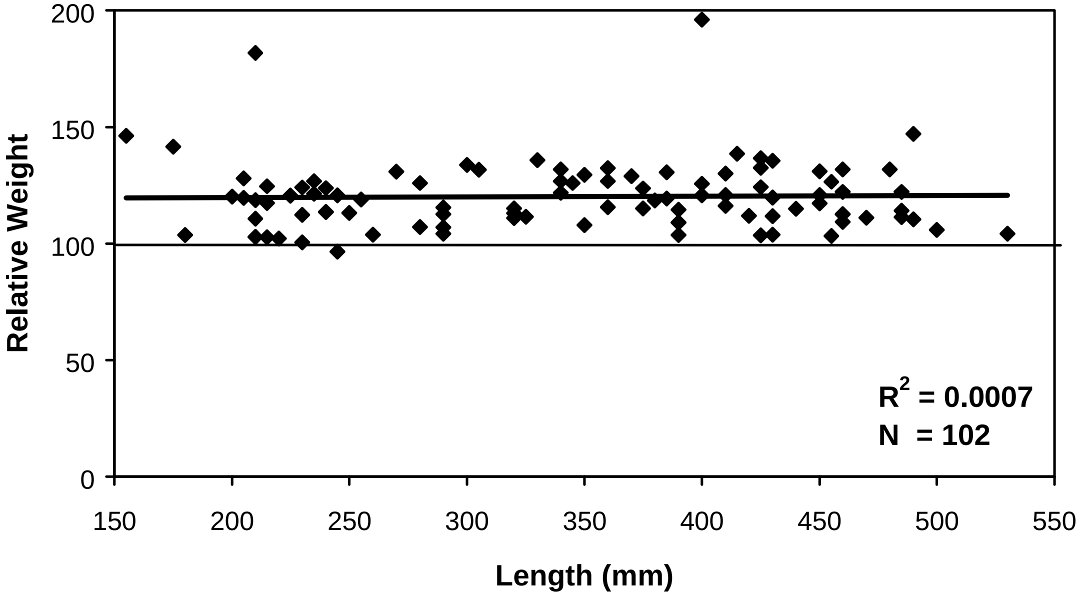

Figure 15. Relative weights of smallmouth bass captured along the western shoreline of Hog Island in 2002. Relative weight of 100 indicates individual was at expected weight-at-length.

Monatu Bay, Sturgeon Bay, St. James Harbor

Population estimates, age-specific mortality rates and relative weights of smb from MON, STUR, and STJ had lower precision than GIH and HOG due to small sample size. Apparent trends in abundance, mortality, condition of smb were lacking, thus data from MON, STUR, and STJ are presented in Appendix I.

Smallmouth Bass Growth

Four hundred and seventy smb were used to determine mean length-at-age in 2001, which ranged from 153 mm at age 2, to 510 at age 13 (Figure 16). Mean length-at-age of smb from the Beaver Archipelago was similar to the predicted values from the von Bertalanffy growth curve (Figure 16). Interestingly, mean length-at-age of smb in 2001 was significantly higher than in 1972 ($t_{0.05, 9} = 1.833$, $t = 4.30$; Figure 17), suggesting that smb were growing at least as well as they were during the peak of the fishery.

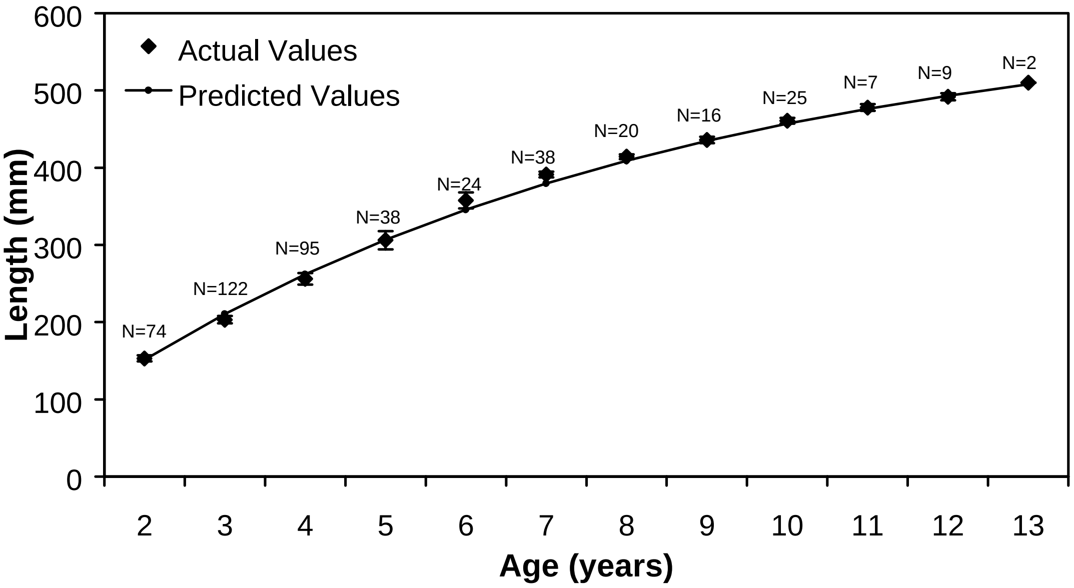

Figure 16. Mean length-at-age (95%confidence intervals) and predicted length-at-age from von Bertalanffy growth equation of smallmouth bass captured in the Beaver Archipelago in 2001. Age 1 smallmouth bass were not captured during sampling.

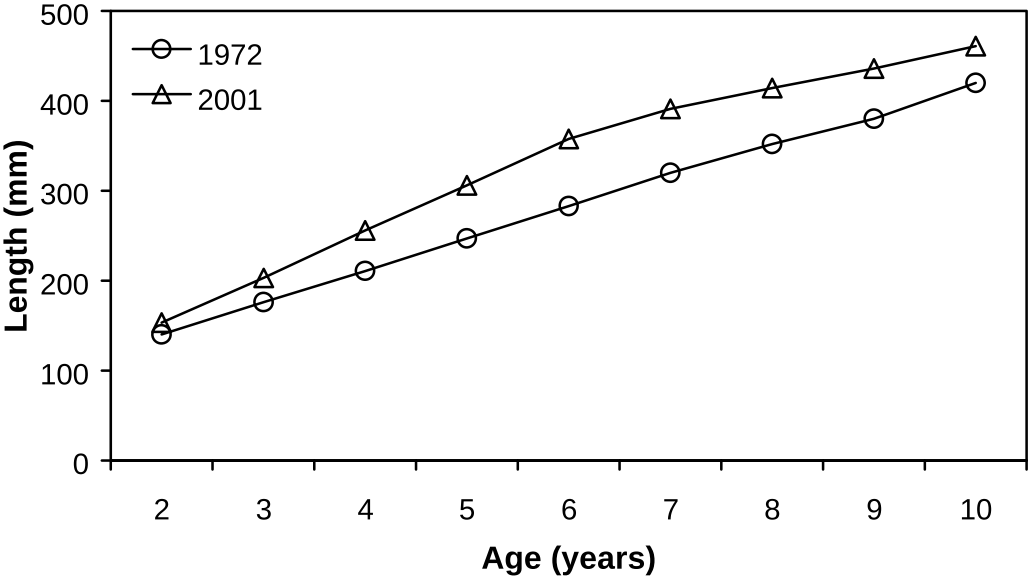

Figure 17. Mean length-at-age for smallmouth bass captured in the Beaver Archipelago in 1972 and 2001. Mean length-at-age in 1972 from Lenon (unpublished data).

CHAPTER 4

DISCUSSION

The most important component of this study was determining smb population size and to compare these estimates with similar estimates conducted in the 1970s and 1980s. Current estimates of abundance were necessary to test the suspicions of the local anglers and to evaluate long-term population trends. Evaluation of the smb population trend in the Beaver Archipelago, however, depended on the precision and accuracy of the population estimates. The accuracy of Schnabel population estimates depends on whether the assumptions of the model were met during sampling (Krebs 1999). The critical assumptions of the Schnabel model relevant to this study were: (1) marked fish do not lose their marks prior to recapture; (2) following release, marked and unmarked fish become randomly mixed; (3) marked and unmarked fish have equal capture probability; and (4) the population is closed with no immigration and emigration (or mortality) (Van Den Avyle and Hayward 1999). Although my analyses suggested that some of these assumptions were violated, the biases from these violations did not significantly affect the estimates obtained in this study. Instead, not only were the violations minimal but ultimately they led to very liberal population estimates.

A linear relationship between the number of marked fish and the proportion of marked fish in the catch was not found consistently in each bay. If the assumptions of the Schnabel estimator were in fact met during sampling, then the relationship would have been linear. As more fish were tagged, the proportion of marked fish in the catch should have increased, unless for example, fish had lost their tags prior to being recaptured and were not recognized as marked. Unfortunately, a nonlinear relationship only signals that one or more assumptions were violated but it does not indicate which assumption was violated or how it was violated (Krebs 1999). Potential violations, therefore, were examined individually to determine how the population estimates were biased.

Tag loss varies depending on the species of fish tagged, the duration of the study, and the experience of the researcher that is tagging (Guy et al. 1996) (Assumption 1). Unfortunately, tag loss for smb was not quantified during this study. In hindsight, tag loss could have been evaluated by applying a second mark to the smb, such as a fin clip. A fin clip would not have healed during the relatively short sample periods in each bay and could not have been lost like an external tag. Furthermore, estimates of tag loss specific to smb were not available in the literature. Gurtin et al. (1999), however, reported tag loss for largemouth bass (*Micropterus salmoides*) was 12% for a six-month period. Given the short sampling periods during this study (7-16 days), tag loss for smb was probably minimal thus not causing severe estimation bias. In any event, substantial tag loss would have caused an under representation of recaptured fish and hence, an overestimation of abundance (Schnabel 1938).

After release, the degree of random mixing of marked and unmarked fish was difficult to determine (Assumption 2), however, marked fish were released in a central location in each bay to increase the likelihood of random mixing. Most smb were not recaptured for several days after initial capture, consequently marked fish probably had ample time to mix freely with unmarked fish. The Schnabel model (M_t), was rarely the most appropriate model of catchability from program CAPTURE, hence marked and unmarked smb usually had unequal catchability (Assumption 3). This potential bias could have been caused by variations in sex, age, spatial distribution, sampling effort, and trap happy or trap shy behavior. Age 2 smb probably had lower catchability than older fish because they were not fully vulnerable to the trap nets, as evidenced by annual length-frequency histograms (Figure10) and a low number of captures. Spatial distribution and sampling effort probably did not cause unequal catchability because the trap nets were evenly distributed throughout the bays. Trap happy or trap shy behavior however, may have caused unequal catchability in some instances. For example, in GIH (2001), several smb were captured more than 10 times during the 14-day sample period, while other individuals were marked and never recaptured. Trap happy behavior of marked individuals would cause an overrepresentation of recaptures, thus underestimating smb abundance. Trap shy behavior of marked individuals was probably more common, thus causing an under representation of recaptures, and an overestimate of population size.

Emigration and immigration of smb during the sample periods was difficult to evaluate in this study (Assumption 4). Initially, I tested this assumption by estimating smb abundance with the Jolly-Seber open population model (Jolly 1965; Seber 1965). Consistent differences between the Jolly-Seber and Schnabel population estimates would have indicated that the smb populations probably were not closed. The Jolly-Seber estimates, however, had wide confidence intervals and were highly variable during the short sampling period; probably due to the unequal catchability and low recaptures (Krebs 1999). Because of these problems, my data did not seem to be appropriate for the Jolly-Seber model and the population estimates it generated were not helpful in evaluating the closed population assumption. Nevertheless, fewer than five tagged smb (all >305 mm) in each year were recaptured in a location other than the bay of their initial capture, indicating that emigration and immigration were probably insignificant. Emigration of marked individuals due to the tagging process most likely caused the violation of the closed population assumption, which would cause an under representation of recaptures, and an over estimate of smb abundance.

Because the assumptions of the Schnabel estimator usually were not met during this study, the population estimates were probably biased. Certainly the estimates, but they were not biased enough to account for an 85% decline in smb since 1972. Furthermore, the potential violations likely caused an overestimate of smb abundance. Therefore, the decline of smb abundance since the 1970s and 1980s may have been greater than what this study quantified.

Trends in mean CPUE closely followed trends in Schnabel population estimates in each bay during this study (e.g. GIH; Figure 18). Catch-per-unit-effort, however, also can be influenced by unequal catchability (Ney 1999). Catch-per-unit-effort was still useful because sampling was standardized during this study, which helps alleviate the effects of unequal catchability. Nevertheless, CPUE data were clearly consistent with trends defined by the population estimates..

Together, the Schnabel estimates and CPUE data both indicate that smb populations of the Beaver Archipelago have stabilized at a new dynamic equilibrium, which is a fraction of historic abundance. Schnabel population estimates from MON, STUR, and STJ fluctuated but did not change significantly within the four years of this study (Appendix I). Estimates from GIH declined significantly from 1999 to 2001 but

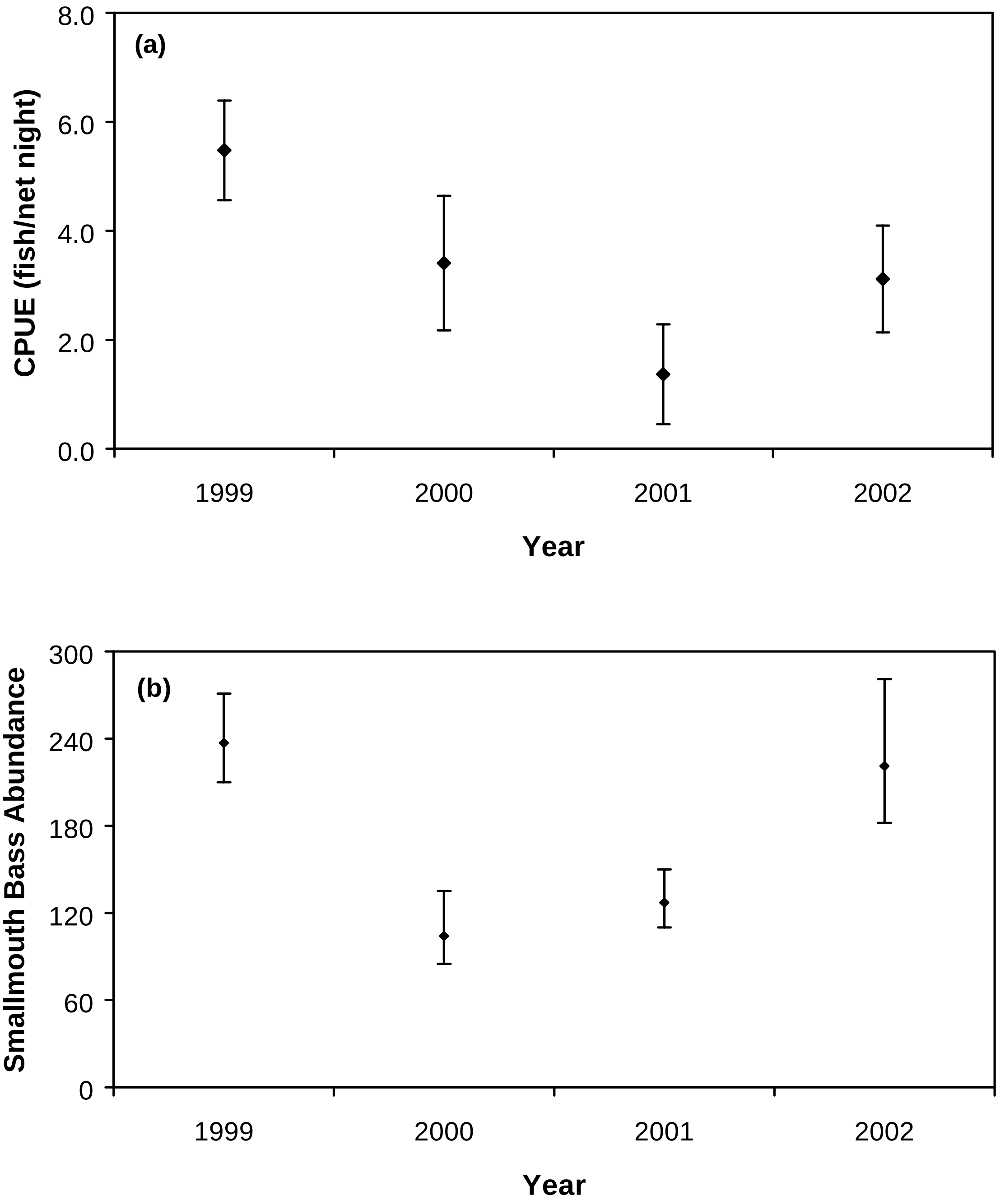

Figure 18. Catch-per-unit-effort (CPUE; 95% confidence intervals) (a) and Schnabel population estimates (95% confidence intervals) (b) of smallmouth bass in Garden Island Harbor, 1999 through 2002.

then increased in 2002. Only population estimates from HOG declined significantly from 1999 through 2002. Although the smb populations in GIH and MON appeared to be generally stable during this study, the Schnabel estimates from those bays had declined 70-95% since the 1980s. Population estimates from STJ were not significantly different from those completed in the 1970s, but changes in smb abundance may not have been detected in STJ due to wide confidence intervals around the estimates (Appendix I). The number of smb that were marked in STJ was similar to that in MON and STUR, yet less than 15% of the marked individuals were recaptured each year, except in 2001. In 2001, the number of recaptures was higher and the confidence intervals were narrower than in all other years. The cause of low recapture probability in STJ, however, was unclear.

Based on the Schnabel population estimates from GIH and MON, the fishery apparently declined during the early 1990s, suggesting that angler harvest probably was not the primary cause. Had angler harvest been substantial enough to limit smb abundance, the decline probably would have started in the 1970s, when the fishery became popular. Because smb are relatively fecund and short-lived (Coble 1975), population size should have increased after angler effort waned in the early 1990s.

While the role of angling in the decline of the fishery was not clear, angler harvest clearly was not limiting smb abundance during this study. In 1999, creel surveys and boat counts were attempted to quantify angler effort and harvest of smb in the Beaver Archipelago. Angler activity, however, was so low that it could not be measured by conventional creel survey methods (D. Peterson, University of Georgia, pers. comm.). Dramatic declines of non-game species paralleling those of smb, also provided indirect evidence that angler harvest was not a major cause of smb declines. If angler harvest was limiting smb populations then rockbass and brown bullhead abundance should have increased as smb declined. Yet, in GIH rockbass and brown bullhead declined 99% from 1984 to 2002. The decline of rockbass and brown bullhead also provided indirect evidence of cormorant predation because the birds commonly consume these species (Ludwig et al. 1989; Neuman et al. 1997; Schneider and Adams 1999)

The decline of the smb fishery appeared to coincide with the rapid increase of nesting cormorants in Michigan during the 1980s and 1990s (Figure 19). Although continuous data of cormorants were not available, the number of nesting pairs in the Beaver Archipelago increased from 880 in 1989 to 11,709 in 1997 (J. Gillingham, Central Michigan University, pers. comm.). During the same period, smb population estimates from GIH declined significantly, but without data from the fishery and cormorant population during the early 1990s, a cause and effect relationship remains speculative.

Age-Specific Mortality Rates

Low smb abundance in the Beaver Archipelago decreased the precision of cohort estimates, and consequently the confidence intervals of the annual mortality rates. Because less than 20 smb were captured from some cohorts, population estimates for younger cohorts were often bracketed by wide confidence intervals. On the other hand, CAPTURE produced estimates with unusually narrow confidence intervals for the older cohorts. For example, in Sturgeon Bay (2000) the age-7 cohort was estimated at 3 (2-4). Only two age-7 smb were captured in Sturgeon Bay (1999) but the likelihood that just four age-7 individuals lived in that bay seems low. Negative annual mortality rates

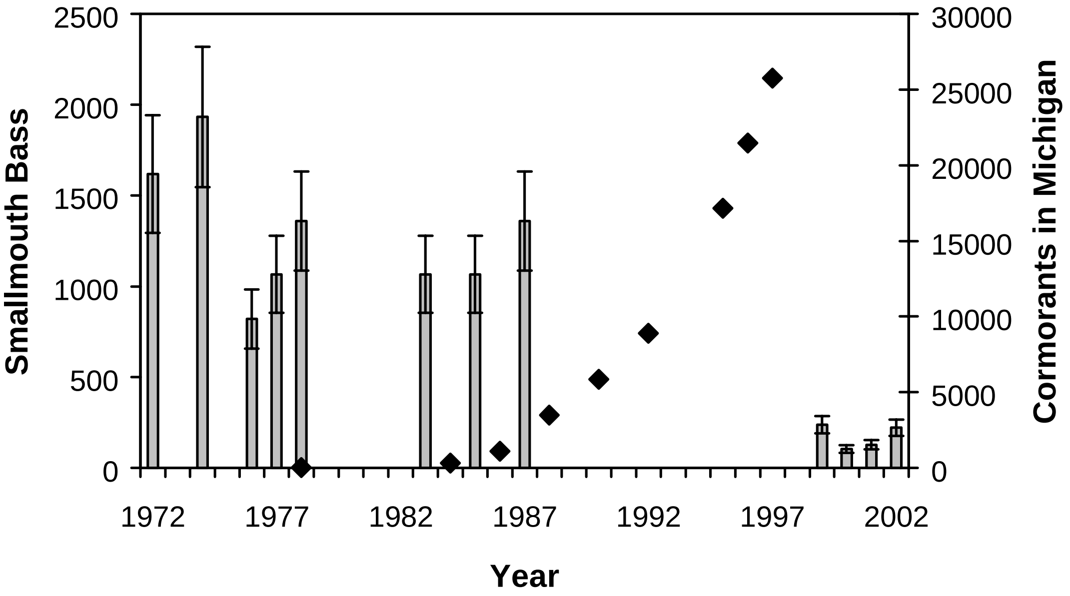

Figure 19. Schnabel population estimates (95% confidence intervals) of smallmouth bass in Garden Island Harbor (bar) and estimated number of nesting pairs of double-crested cormorants in Michigan (Ludwig and Summer 1997) (diamond), 1972-2002. Population estimates from 1972 through 1987 from Lenon (unpublished data). Fisheries data were not collected from 1988 through 1998.

(indicating cohort growth) also were common in some older cohorts. This was most likely an artifact of the wide confidence intervals caused by low population size of smb.

The best annual cohort mortality rates were obtained from the largest remaining smb populations (GIH and HOG) from 1999 to 2000 and 2000 to 2001. In those years, mortality rates for smb ages 3-5 were 50-99%, a level unprecedented when compared to other smb fisheries. Reed and Rabeni (1989) estimated that total annual mortality for smb ages 3-7 was 16% in several unexploited (no angling) streams in Missouri. Coble (1975) reported natural mortality rates ranging from 12.5-43% among smb populations in Wisconsin. Because fishing activity was virtually nonexistent in the Archipelago, smb mortality documented in this study was likely caused by natural factors. This conclusion is further supported by the angling regulations, which set a minimum length limit of 350 mm TL, a size obtained at age-6 and age-7.

Annual mortality rates in GIH and HOG, together with the length-frequency histograms suggest that many smb 150-300 mm were lost from 1999 to 2000 and again from 2000 to 2001. Previous studies have shown that fish in this size range are preferred prey of cormorants (Craven and Lev 1987; Hobson et al. 1989; Campo et al. 1993; Modde et al. 1996; Neuman et al. 1997; Adams et al. 1999; Johnson et al. 2002). Predation may also have caused the unusually high juvenile smb mortality; and some piscivorous predators were caught in the bays including northern pike (*Esox lucius*) and bowfin (*Amia calva*). The scarcity of these species, however, seems to preclude this possibility as less than 10 pike or bowfins were captured in each year of this study.

Although annual mortality rates of smb were not estimated in past surveys, catch data from 1972 indicated that adult survival was lower than during this study. Trap net catch data from 1972 rarely included smb greater than the minimum length limit (255 mm) (Lenon, unpublished data), indicating that adult survival was low. “Stockpiling” of smb just below the minimum length-limit is characteristic of heavily exploited recreational fisheries (Coble 1975). Given the supposed popularity of the fishery during the 1970s, adult survival was probably suppressed by angler harvest during this period. The cumulative effect that angler harvest had on the smb population in the Beaver Archipelago, however, remains speculative; but clearly angling mortality is not currently limiting the smb population.

Condition and Growth

Mean relative weights for each bay were 20-56% higher than the standard value (100) in 2002, indicating that resource availability was not limiting. Although mean relative weight was significantly different among the bays, all means were significantly higher than 100. These data clearly indicate that the smb population was not resource limited during this study.

Mean length-at-age also indicated that resource availability for smb was not limiting. Although Lake Michigan has a shorter growing season and cooler summer water temperatures than other lakes inhabited by other smb populations, smb mean length-at-age from the Beaver Island population met or exceeded the predicted values from the von Bertalanffy growth curve. Furthermore, mean length-at-age from 2001 was significantly higher than in 1972, suggesting that the smb growth has increased as the population has declined (compensatory response). These data also suggest that food resources were not limiting the smb population during this study.

Because 78 smb retained their t-bar tags for at least two successive years during this study, a direct measure of growth also was possible. Direct measurements of growth were compared to values from the 1970s (Lenon, unpublished data) (Figure 20). Juvenile growth was higher during this study, again, probably a compensatory response to lower abundances. The stockpiling of smb, just below the 1970 minimum length limit (255 mm) probably increased intraspecific competition during the height of fishery. Although speculative, this would explain why juvenile growth rates were higher in this study.

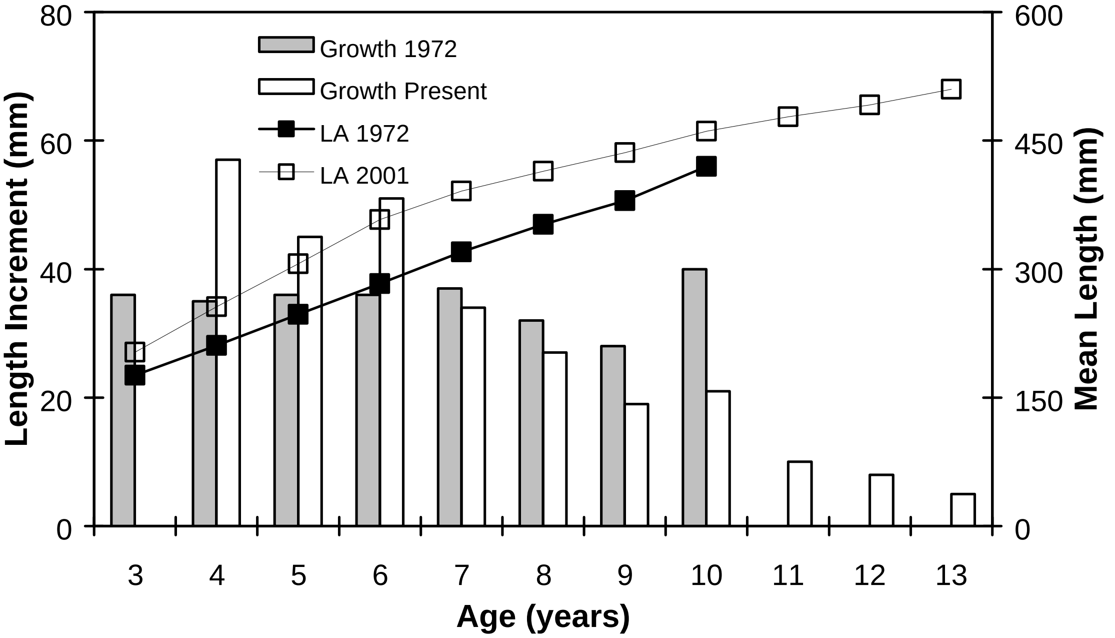

Figure 20. Mean length-at-age (LA) and growth increments of smallmouth bass in the Beaver Archipelago from 1972 and 2001. Mean length-at-age for 1972 from Lenon (unpublished data).

Current Status of Smallmouth Bass

The smb population of the Beaver Archipelago appeared to be limited by unusually high juvenile mortality rates during the four years of this study. High adult survival rates, low angler effort, and a 73-99% decline of sympatric nongame species provides strong evidence that angling was not limiting smb abundance. Excellent growth and condition of smb suggests that resource availability was not limiting juvenile survival. Given the relatively high rates of juvenile mortality detected in this study, cormorant predation was the most obvious and most likely factor limiting smb abundance.

Declines of the smb populations in eastern Lake Ontario were conspicuously similar to those documented in this study. Both fisheries declined precipitously during a period of rapid increase in nesting cormorants during the early 1990s (Lantry et al. 2002). Growth and condition of smb improved since the 1970s, suggesting that ecological changes in Lake Ontario and Lake Michigan had not affected the smb stocks. Unusually high juvenile mortality rates also were found in both cases; strongly implicating cormorant predation. Unlike the Beaver Islands however, cormorant diet analyses were done throughout the decline of the smb fishery in eastern Lake Ontario, where direct evidence from cormorant diets supported the conclusion that cormorant predation was limiting the smb population.

All fisheries data collected in this four-year study provided strong circumstantial evidence that cormorant predation was a major factor in the decline of the Beaver Islands smb fishery, but without cormorant diet data from the early 1990s, direct physical evidence is lacking. Ludwig (1989) however, reported that from 1986-1989 smb constituted 1-9% of prey biomass consumed by cormorants nesting within the Archipelago. During that study, approximately 880 cormorants nested in the Archipelago (J. Gillingham, Central Michigan University, pers. comm.) residing there for about 180 days. Each bird typically consumes 0.25-0.5 kg of fish per day (Shramm et al. 1984; Shramm et al. 1989), thus roughly 792 kg of smb was were consumed. My data show that the mean weight of a 200 mm smb (cormorant preferred prey size) during this study was 150 g. If we assume that this was the average size of smb eaten in 1989, the number of smb consumed by cormorants would have been at least 5280. In 1987, Lenon (unpublished data) estimated smb abundance in GIH was between 1200-1400 fish.

Hence, a cormorant predation rate as low as 1% could have been solely responsible for the smb decline. This scenario is purely speculative, yet is illustrates the potential effect of a large cormorant population on a relatively small smb population.

Fellow researchers sampled cormorant stomach contents in 2001 to quantify the current consumption rates in the Beaver Islands. With approximately 25,000 cormorants and less than 2,000 (<1,500 of optimal prey size) smb, however, the probability of finding direct evidence of predation was low. Despite the unlikelihood, one smb was recovered from the 50 cormorant stomachs that were examined (J. Gillingham, Central Michigan University, pers. comm.). Although this finding does in fact provide direct evidence of predation, calculations of cormorant predation based on these data are unrealistically high. If for example, the total stomach contents of the 50 cormorants represents one day of feeding and one of every 50 cormorants ate one smb each day; then the cormorant population would have consumed approximately 400 smb per day. Because cormorants nest in the Archipelago for approximately 180 days the cormorant stomach data would yield an estimate of 72,000 smb consumed by cormorants in 2001. Given that my estimate of the entire smb population for all bays combined was only about 2,000 fish in 2001, the estimate of cormorant predation on smb is obviously too high. Nevertheless, these findings illustrate that even when cormorant consumption rates are relatively low, a fishery might be dramatically affected.

Cormorants appear to concentrate their feeding in the shallow bays of the Beaver Archipelago. First, because the largest nesting colonies are situated in a central position within the Archipelago, the bays are within a short distance (1-2 km) for foraging cormorants (Figure 21). Second, during sampling I consistently observed 10-15

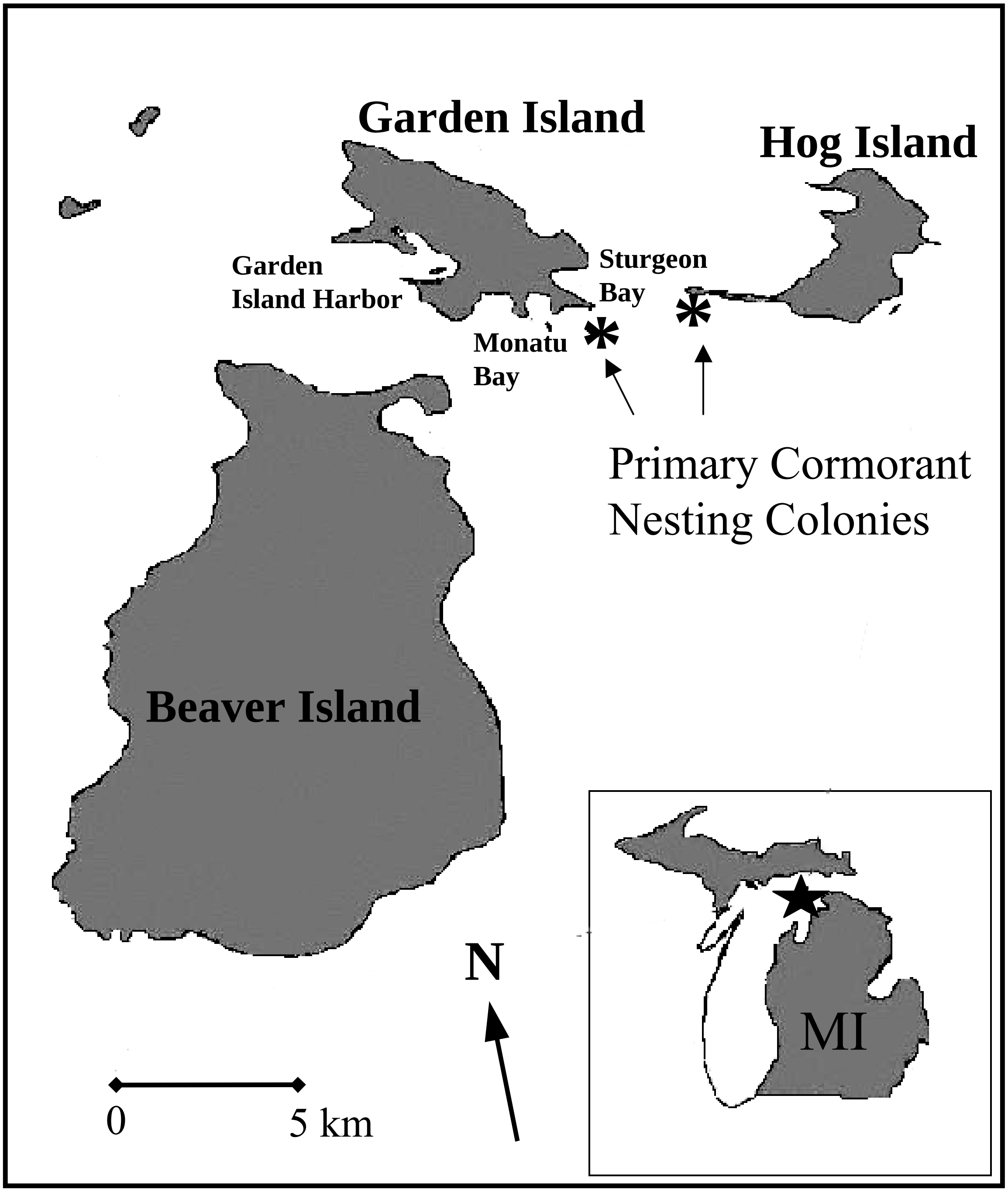

Figure 21. Primary locations of double-crested cormorant nesting colonies in the Beaver Archipelago. Primary colonies had 3,181 nesting double-crested cormorants in 2001 (J. Gillingham, Central Michigan University, pers. comm.).

cormorants each day swimming on the surface or gathered on rock spits in GIH and HOG, indicating that the birds were, in fact, feeding in and around the bays. Third, Gillingham and Seefelt (2001) reported that crayfish constitute as much as 24% of cormorant's diet, which further indicates that cormorants often feed in shallow water habitat also preferred by smb. According to the optimal foraging theory (MacArthur and Pianka 1966), cormorants should feed on almost anything edible they encounter while hunting. If cormorants often feed in shallow water habitat, as indicated by the abundance of crayfish in their diets, then they would likely consume smb as well.

Implications of this study

The extent to which cormorant predation has caused the decline of the smb fishery in the Beaver Archipelago cannot be conclusively determined without population and diet data on both species during the actual decline of smb numbers. Although angler harvest may have contributed to the decline in smb abundance, anecdotal evidence and low angler effort documented in this study suggests that angler effort was waning during the period that smb abundance was declining. While direct quantified evidence of cormorant predation is now virtually impossible to obtain, all smb data collected in this study suggested that cormorants not only caused the smb decline in the Beaver Archipelago but they are now limiting smb recovery as well.

If cormorant predation is limiting smb abundance, what potential management actions could be implemented to recover smb in the Beaver Archipelago? Many islanders have insisted that killing cormorants is the only way to restore the smb fishery. Given the current abundance of cormorants, this strategy would require that thousands of birds be killed annually which might prove difficult if not impossible. Another potential management strategy is to prevent cormorants from nesting or to spray their eggs with vegetable oil to reduce reproductive success. Nesting cormorants also are extremely sensitive to disturbance leaving their nest at the first sight of human intrusion. The resulting egg or chick predation by gulls nesting nearby would likely reduce cormorants breeding success even further (Duffy 1995) if colonies were regularly harassed during nesting. Farquhar et al. (2000) found that removing cormorant nests from colonies or treating the nests with pure food grade corn oil effectively eliminated cormorant reproductive output. These strategies, however, are expensive long-term programs. For example, nest disturbance or egg oiling would need to be done several times during the nesting period. These practices would also need to be done each year to prevent recolonization.

Given the current disparity between smb and cormorant populations, future research should focus on manipulative experiments to better quantify the effects of cormorant predation on fish populations. In the Beaver Islands, cormorant reproduction could be reduced by regular harassment of the breeding colonies or nest destruction. With baseline data from this study, the changes in smb population dynamics could be evaluated to determine the effectiveness of these treatments. Although a manipulative study would be expensive and logistically complicated, the data collected would be more quantified than observational studies that have been conducted thus far.

The results of this study may contribute to the reevaluation of the effects imposed by cormorants on local fisheries. Previous diet analyses of cormorants in the Great Lakes concluded that the birds do not affect gamefish populations (Craven and Lev 1987; Hobson et al. 1989; Ludwig et al. 1989; Neuman et al. 1997). Like the research on Lake

Ontario cormorants, this study illustrates the importance of collecting fisheries data when trying to evaluate the effects of cormorant predation. Furthermore, the similarity between the decline of the smb fisheries in the Beaver Islands and that observed in eastern Lake Ontario indicates that cormorant predation can have dramatic effects on local fisheries. Thus, biologists must now recognize that the current abundance of cormorants in the Great Lakes may be adversely affecting many important local fisheries.

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APPENDEX I

Table A1. Catch statistics, catch-per-unit-effort (CPUE; 95% confidence intervals), and population estimates (95% confidence intervals) of smallmouth bass in Monatu Bay, 1999 through 2002. CPUE followed by the same lowercase letter are not significantly different ($\alpha = 0.05$) based on Tukey's post hoc test.

Year	Total captures[1]	Catch-per-unit-effort	Total marked	Total recaptures	Schnabel (N)	CAPTURE (N)
1999	92	5.7^a (3.7-7.7)	55	35	81 (61-121)	94 (77-129)
2000	68	4.8^a (2.6-7.1)	47	21	72 (47-115)	70 (53-114)
2001	90	4.6^a (2.5-6.6)	45	36	64 (48-95)	43 (42-44)
2002	109	6.7^a (4.7-8.7)	53	51	69 (54-94)	73 (60-107)

[1] Total captures included both marked and unmarked individuals.

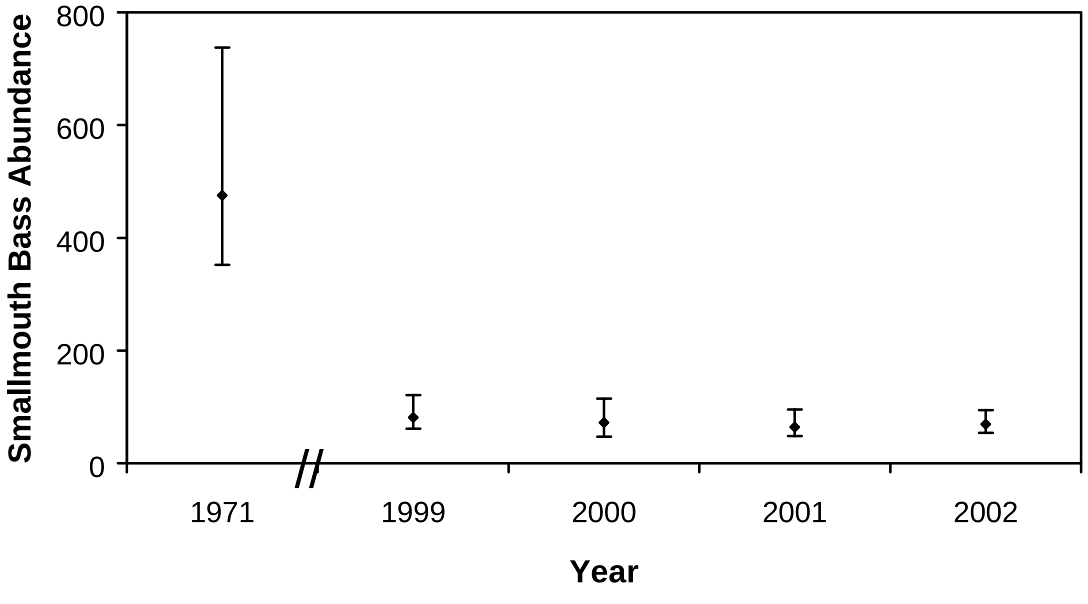

Figure A1. Schnabel population estimates (95% confidence intervals) of smallmouth bass in Monatu Bay, 1999 through 2002. Population estimate from 1971, Lenon (unpublished data) shown for comparison.

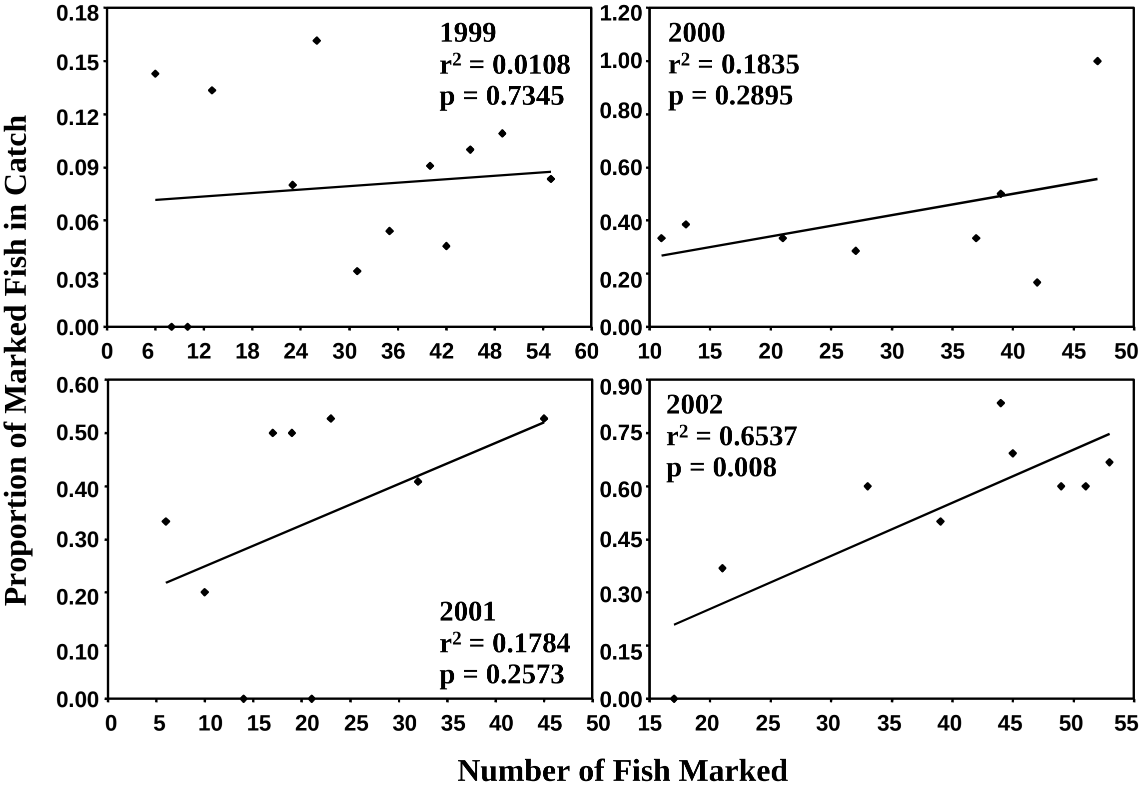

Figure A2. Regression analyses of smallmouth bass capture data from Monatu Bay, 1999 through 2002. A linear relationship ($p < 0.05$) indicated that the assumptions of the Schnabel population estimator were met during sampling.

Table A2. Estimates of cohort abundance (95% confidence intervals) of smallmouth bass from Monatu Bay, 1999 through 2002. Cohort ABUNDANCE of age 1 and 2 was not estimated and ages 8 through 13 were combined.

	Schnabel Model				Program CAPTURE			
Age	1999	2000	2001	2002	1999	2000	2001	2002
3	25	34	17	16	21	22	20	6
	(11-67)	(18-78)	(6-85)	(3-160)	(17-41)	(21-23)	(13-52)	(6-8)
4	27	3	32	29	27	3	8	34
	(16-50)	(1-12)	(6-163)	(13-80)	(22-45)	(2-5)	(7-24)	(23-63)
5	27	5	6	9	25	5	6	11
	(14-63)	(2-25)	(3-15)	(5-19)	(19-45)	(4-21)	(5-7)	(10-46)
6	3	9	2	5	2	8	3	3
	(1-30)	(3-43)	(1-7)	(1-50)	(1-22)	(7-21)	(2-4)	(2-7)
7	*	2	1	7	*	4	1	6
	*	(1-15)	(1-10)	(4-17)	*	(3-18)	(1-2)	(5-9)
8-13	10	1	9	12	4	1	11	9
	(2-100)	(1-10)	(4-37)	(5-37)	(3-21)	(1-2)	(9-26)	(8-25)

*Age 7 smallmouth bass were not captured

Table A3. Annual age-specific mortality rates (95% confidence intervals) of smallmouth bass in Monatu Bay, 1999 through 2002. Cohort abundance of age 1 and 2 was not estimated and ages 8 through 13 were combined.

	Schnabel Model			Program CAPTURE		
Age	1999-2000	2000-2001	2001-2002	1999-2000	2000-2001	2001-2002
3	0.88	0.05	-0.71	0.86	0.63	-0.70
	(-0.09-0.99)	(-8.06-0.92)	(-1.23-0.85)	(0.70-0.95)	(-0.14-0.69)	(-3.85-0.56)
4	0.81	-1.00	0.72	0.81	-1.00	-0.38
	(-0.56-0.96)	(-1.40-0.75)	(-2.17-0.96)	(0.04-0.91)	(-2.50-0.00)	(-5.57-0.58)
5	0.67	0.60	0.17	0.68	0.40	0.50
	(-2.07-0.95)	(-2.50-0.96)	(-1.57-0.93)	(-0.10-0.84)	(0.00-0.90)	(-0.40-0.71)
6	0.33	0.89	-1.50	-1.00	0.87	-1.00
	(1.40-0.97)	(-2.33-0.97)	(-2.50-0.43)	(-8.00-0.86)	(0.71-0.95)	(-3.50-(-)0.25)
8-13	0.90	-4.00	-0.33	0.75	-1.00	0.18
	(-4.00-0.97)	(-8.00-0.60)	(-8.25-0.86)	(0.33-0.95)	(-2.50-(-)0.01)	(-1.78-0.69)

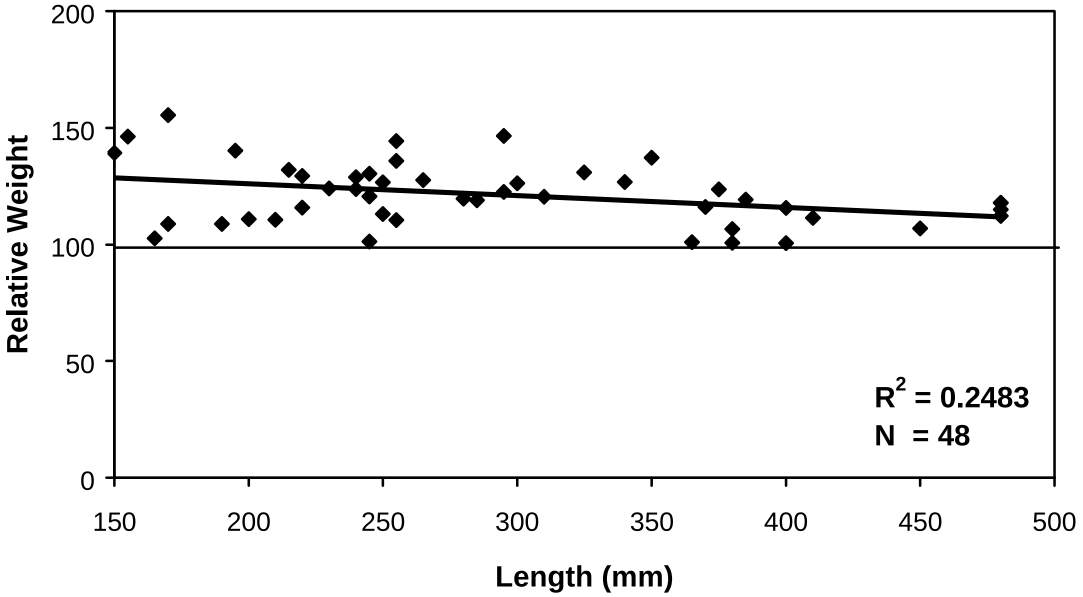

Figure A3. Relative weights of smallmouth bass captured in Monatu Bay in 2002. Relative weight of 100 indicates individual was at expected weight-at-length.

Table A4. Catch statistics, catch-per-unit-effort (CPUE; 95% confidence intervals), and population estimates (95% confidence intervals) of smallmouth bass in Sturgeon Bay, 1999 through 2002. CPUE followed by the same lowercase letter are not significantly different (α = 0.05) based on Tukey's post hoc test.

Year	Total captures[1]	Catch-per-unit-effort	Total marked	Total recaptures	Schnabel (N)	CAPTURE (N)
1999	105	3.9[a]	57	45	75	115
		(2.8-5.0)			(58-105)	(94-154)
2000	102	5.2[a]	64	37	97	65
		(3.9-6.6)			(77-131)	(64-66)
2001	90	2.9[a]	51	33	81	71
		(1.7-5.1)			(60-123)	(59-96)
2002	83	3.9[a]	51	31	72	73
		(2.7-5.1)			(63-110)	(60-107)

[1] Total captures included both marked and unmarked individuals.

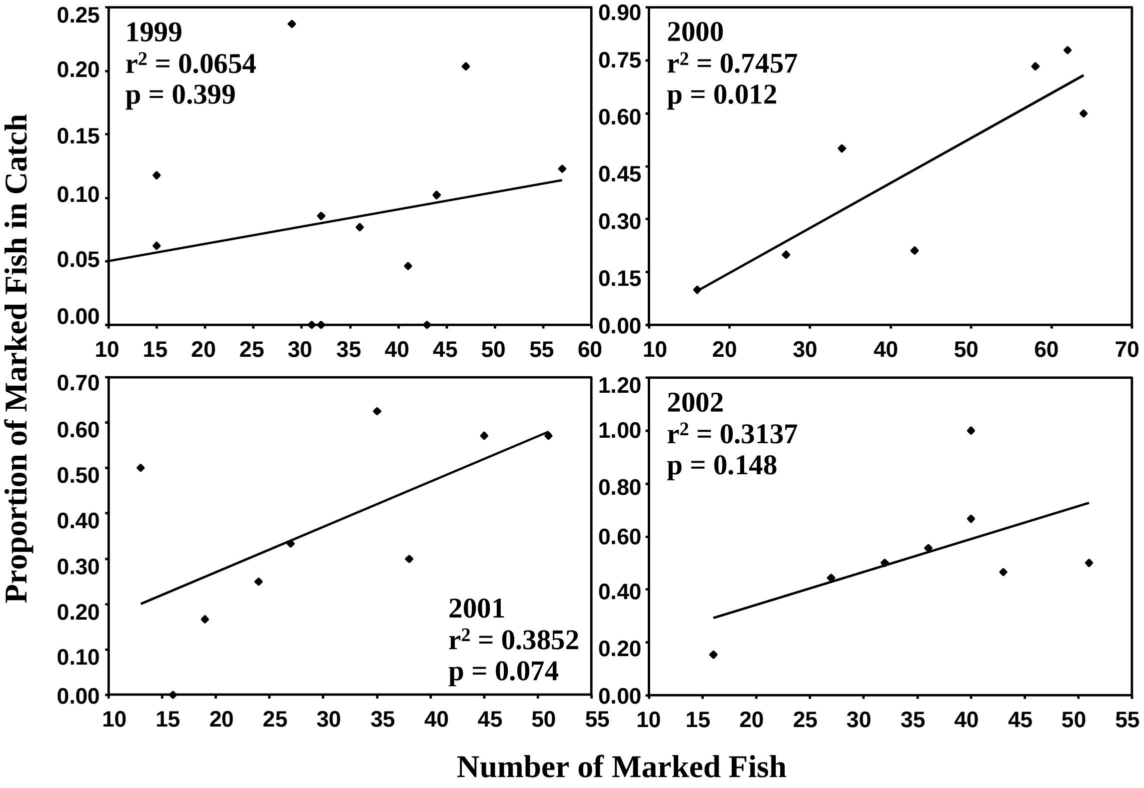

Figure A4. Regression analyses of smallmouth bass capture data from Sturgeon Bay, 1999 through 2002. A linear relationship ($p < 0.05$) indicated that the assumptions of the Schnabel population estimator were met during sampling.

Table A5. Estimates of cohort abundance (95% confidence intervals) of smallmouth bass in Sturgeon Bay, 1999 through 2002. Cohort abundance of age 1 and 2 was not estimated and ages 8 through 13 were combined.

	Schnabel Model				Program CAPTURE			
Age	1999	2000	2001	2002	1999	2000	2001	2002
3	45	64	37	12	38	37	29	21
	(22-112)	(40-112)	(18-92)	(6-33)	(28-71)	(36-38)	(23-48)	(15-42)
4	35	10	12	24	33	8	8	23
	(19-79)	(5-24)	(4-65)	(4-153)	(26-55)	(7-15)	(7-24)	(10-105)
5	8	8	1	7	9	5	2	6
	(4-20)	(2-75)	(1-20)	(3-21)	(8-17)	(4-20)	(1-20)	(5-22)
6	2	9	6	5	3	4	5	4
	(1-20)	(2-90)	(1-60)	(2-23)	(2-9)	(3-5)	(4-13)	(3-12)
7	3	4	7	9	5	3	7	5
	(1-30)	(1-40)	(4-16)	(3-90)	(4-13)	(2-4)	(6-14)	(4-6)
8-13	10	3	7	13	12	2	7	11
	(4-52)	(1-30)	(3-29)	(7-28)	(9-31)	(1-20)	(6-17)	(10-12)

Table A5. Annual age-specific mortality rates (95% confidence intervals) of smallmouth bass in Sturgeon Bay, 1999 through 2002. Cohort abundance of age 1 and 2 was not estimated and ages 8 through 13 were combined.

	Schnabel Model			Program CAPTURE		
Age	1999-2000	2000-2001	2001-2002	1999-2000	2000-2001	2001-2002
3	0.78	0.81	0.35	0.79	0.78	0.21
	(-0.09-0.95)	(-0.62-0.96)	(-7.50-0.95)	(0.46-0.90)	(0.33-0.81)	(-3.56-0.79)
4	0.78	0.90	0.41	0.85	0.75	0.25
	(-2.94-0.97)	(-3.00-0.96)	(-4.25-0.95)	(0.23-0.92)	(-1.86-0.93)	(-2.14-0.79)
5	-0.12	0.25	-2.00	0.56	0.00	-1.00
	(-2.15-0.90)	(-2.90-0.99)	(-4.00-0.90)	(0.37-0.82)	(-2.25-0.80)	(-1.10-0.85)
6	-1.00	0.22	-0.50	0.00	-0.75	0.00
	(-3.90-0.95)	(-7.00-0.96)	(-8.90-0.95)	(-1.00-0.78)	(-3.67-0.20)	(-0.50-0.69)
8-13	0.70	-1.33	-0.86	0.83	0.70	-0.57
	(-6.50-0.98)	(-2.80-0.90)	(-8.33-0.75)	(-1.22-0.97)	(-2.50-(-)1.00)	(-1.00-0.41)

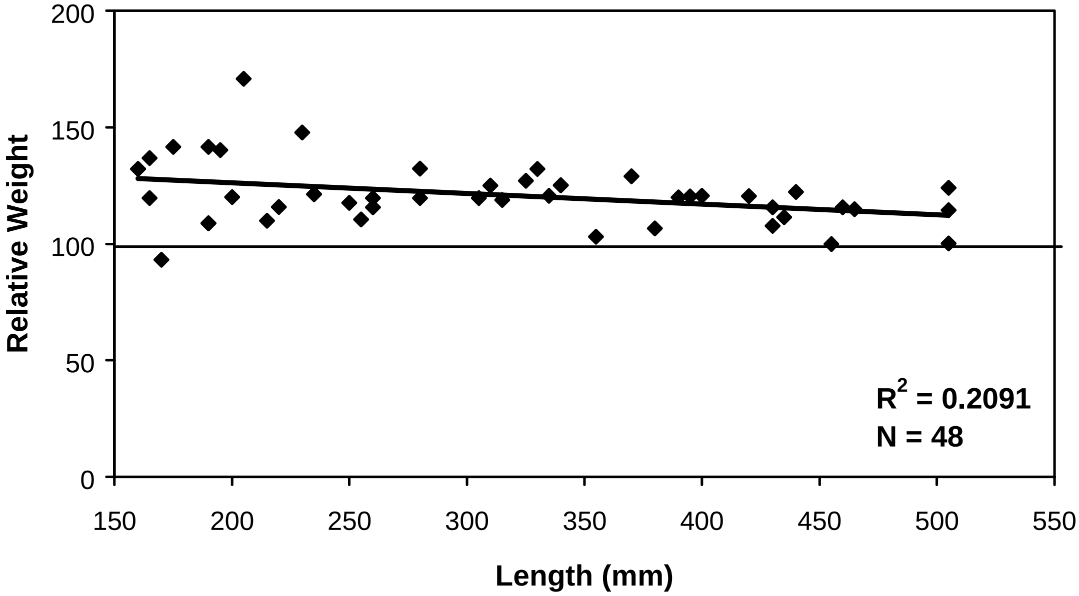

Figure A5. Relative weights of smallmouth bass captured in Sturgeon Bay in 2002. Relative weight of 100 indicates individual was at expected weight-at-length.

Table A6. Catch statistics, catch-per-unit-effort (CPUE; 95% confidence intervals), and population estimates (95% confidence intervals) of smallmouth bass in St. James Harbor, 1999 through 2002. CPUE followed by the same lowercase letter are not significantly different ($\alpha = 0.05$) based on Tukey's post hoc test.

Year	Total captures	Catch-per-unit-effort	Total marked	Total recaptures	Schnabel (N)	CAPTURE (N)
1999	75	2.2[a]	60	9	249	44
		(0.4-4.0)			(131-561)	(43-45)
2000	78	3.9[a]	61	11	170	133
		(1.9-5.9)			(95-346)	(94-218)
2001	108	5.1[a]	65	42	81	64
		(3.1-7.2)			(70-130)	(63-70)
2002	54	3.0[a]	38	7	151	234
		(1.0-5.0)			(86-581)	(115-564)

[1] Total captures included both marked and unmarked individuals.

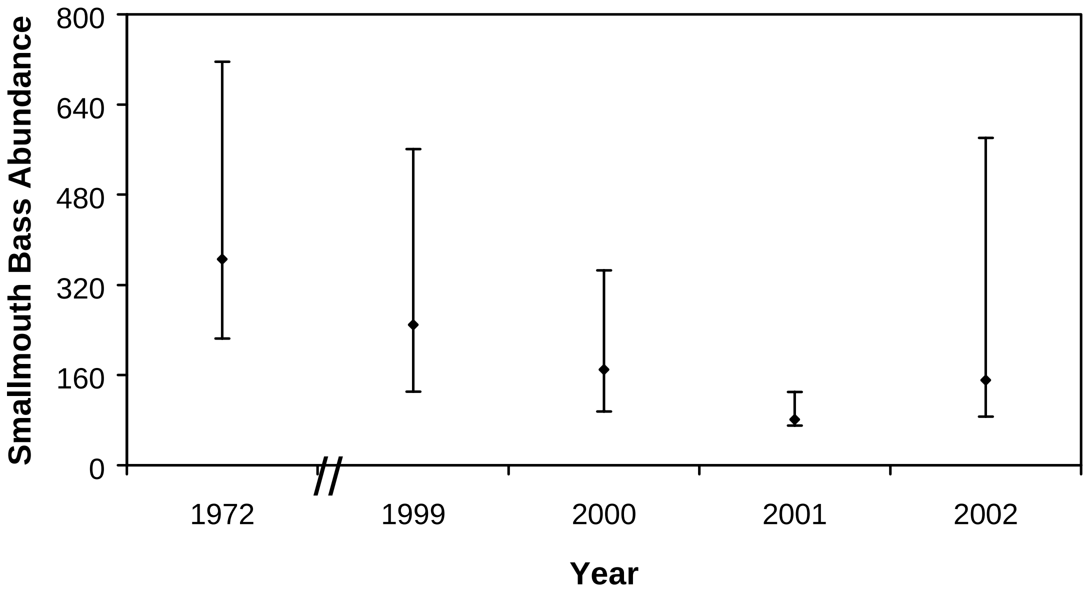

Figure A6. Schnabel population estimates (95% confidence intervals) of smallmouth bass in St. James Harbor, 1999 through 2002. Population estimate for 1972 from Lenon (unpublished data) shown for comparison.

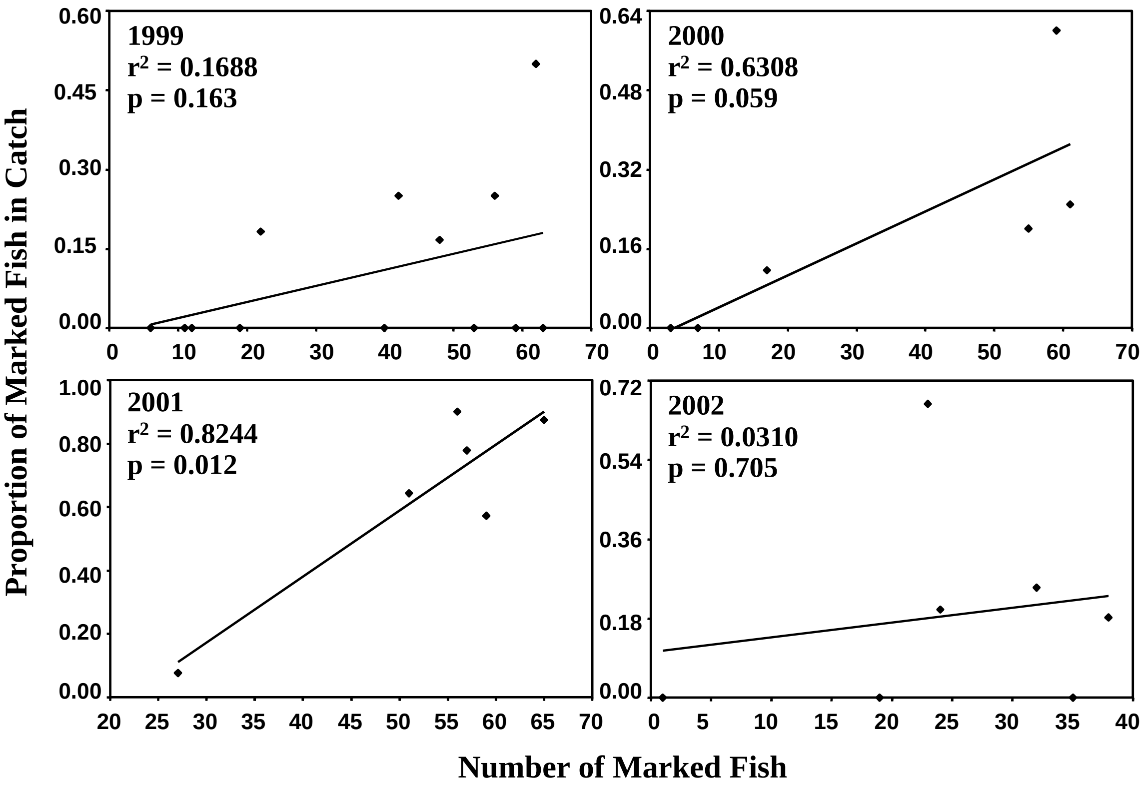

Figure A7. Regression analyses of smallmouth bass capture data from St. James Harbor, 1999 through 2002. A linear relationship ($p < 0.05$) indicated that the assumptions of the Schnabel population estimator were met during sampling.

Table A7. Estimates of cohort abundance (95% confidence intervals) of smallmouth bass in St. James Harbor, 1999 through 2002. Cohort abundance of age 1 and 2 was not estimated and ages 8 through 13 were combined.

	Schnabel Model				Program CAPTURE			
Age	1999	2000	2001	2002	1999	2000	2001	2002
3	69	32	24	5	37	52	20	4
	(12-690)	(15-79)	(15-40)	(1-50)	(23-68)	(35-99)	(19-21)	(3-17)
4	47	146	38	233	30	121	25	132
	(8-470)	(26-275)	(22-72)	(42-503)	(19-59)	(41-542)	(24-28)	(52-443)
5	22	79	3	37	25	43	8	32
	(7-112)	(14-790)	(1-25)	(10-365)	(18-46)	(28-75)	(7-9)	(22-58)
6	5	8	2	5	6	3	2	4
	(2-45)	(2-80)	(1-10)	(1-50)	(5-13)	(2-11)	(1-3)	(3-7)
7	10	5	3	*	4	4	2	*
	(2-10)	(1-50)	(1-30)	*	(3-18)	(3-17)	(1-3)	*
8-13	6	3	6	3	2	2	5	5
	(1-60)	(1-30)	(2-55)	(1-30)	(1-20)	(1-18)	(4-6)	(4-12)

*Age 7 smallmouth bass were not captured

Table A8. Annual age-specific mortality rates (95% confidence intervals) of smallmouth bass in St. James Harbor, 1999 through 2002. Cohort abundance of age 1 and 2 was not estimated and ages 8 through 13 were combined.

	Schnabel Model			Program CAPTURE		
Age	1999-2000	2000-2001	2001-2002	1999-2000	2000-2001	2001-2002
3	-1.11	-0.18	-1.70	-2.27	0.52	-0.56
	(-1.20-0.96)	(-3.80-0.72)	(3.20-(-)0.05)	(-3.25-0.39)	(0.20-0.76)	(-2.23-(-)1.47)
4	-0.68	0.98	0.03	-0.43	0.93	-0.28
	(-9.70-0.97)	(0.04-0.99)	(-1.56-0.86)	(-2.95-0.52)	(0.78-0.98)	(-1.42-0.21)
5	0.63	0.97	-0.67	0.88	0.95	0.50
	(-1.04-0.98)	(0.29-0.99)	(-4.90-0.96)	(0.39-0.96)	(0.89-0.99)	(0.00-0.67)
6	0.00	0.62	*	0.33	0.33	*
	(-2.40-0.97)	(-1.40-0.99)	*	(-2.40-0.77)	(-0.50-0.91)	*
8-13	0.50	-1.00	0.50	0.00	-1.50	0.00
	(-2.90-0.98)	(-5.40-0.93)	(-1.40-0.98)	(-1.70-0.95)	(-5.00-0.78)	(-2.00-0.33)

*Annual mortality rate was not determined because age 7 smallmouth bass were not captured in 2002.

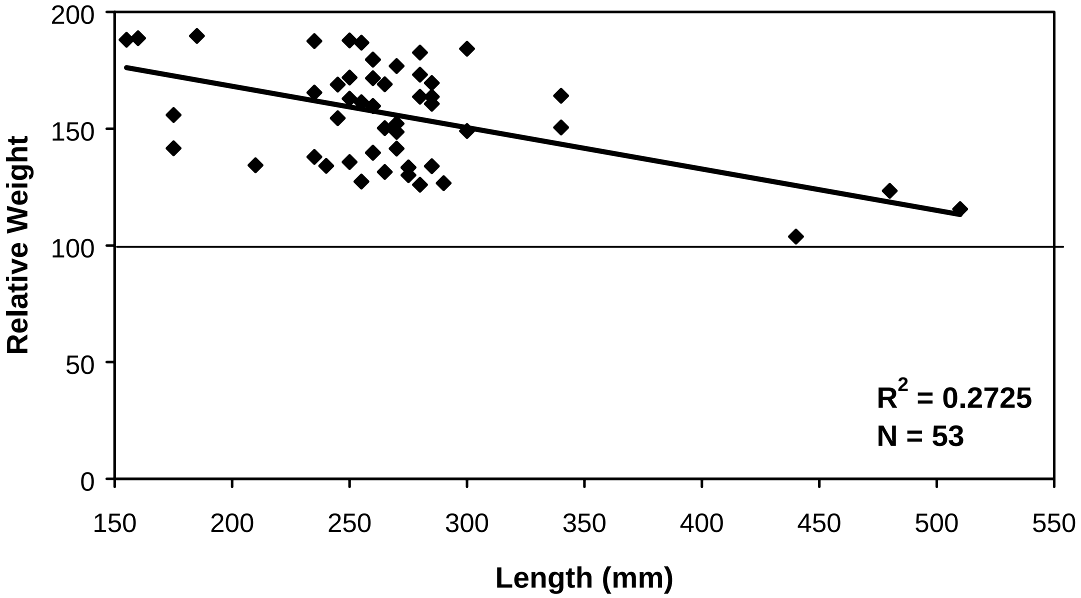

Figure A8. Relative weights of smallmouth bass captured in St. James Harbor in 2002. Relative weight of 100 indicates individual was at expected weight-at-length.