

AN EVALUATION OF SYSTEMATIC ERROR IN THE
ESTIMATION OF FISH POPULATION SIZE

by

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INTRODUCTION

Accurate estimation of animal population size has challenged biologists since the earliest attempts were made to scientifically manage wildlife resources. Walton (1653) first recorded efforts to estimate fish populations. He reported that Sir Francis Bacon studied salmon populations by marking fish and making observations on their migrations and relative numbers. Estimation of fish populations, however, did not become a common scientific procedure until late in the nineteenth century. Petersen (1896) is given credit for developing single census mark and recapture methods for use in fisheries research. Procedures outlined by Petersen remained relatively unchanged until the middle of the twentieth century when quantitative sciences became more sophisticated and development of more complex models began. Some investigators offered modifications to the Petersen method in order to eliminate theoretical bias (Bailey, 1951; Chapman, 1951; Schaefer, 1951; Chapman and Junge, 1956). Other investigators proposed new estimation procedures. Modification of the Petersen estimator to allow for continuous marking resulted in development of multiple census methods (Schnabel, 1938; Schumacher and Eschmeyer, 1943; Chapman, 1952; Jolly, 1965; Robson and Regier, 1971). Catch per unit of effort data was also developed into estimation models (Leslie, 1939; DeLury, 1947; Zippin, 1958; Seber and Le Cren, 1967).

In recent years, major contributions to the field of population estimation has been elimination of theoretical errors. Bailey (1952)

reported that the Petersen estimator theoretically overestimates actual population size by a factor of $1/r$, where r is the number of recaptures. With a reasonable number of recaptures, a positive bias of $1/r$ would be insignificant and of little concern to a fisheries manager. By contrast, several recent studies have shown that populations of warmwater gamefish are often underestimated by factors of $1/3$ to $2/3$ (Carlander and Lewis, 1948; Fredin, 1950; Lawrence, 1952; Carlander and Moorman, 1956; Loeb, 1958; Isaac and Bond, 1963; Buck, 1965). Buck (1965) estimated fish populations from fifteen one-acre ponds. Despite using seines which encompassed the entire pond, most species present were significantly underestimated. Buck concluded that the problem was not mathematical. Development of complex, theoretically unbiased estimators is of little value when applied to biological situations of essentially unknown characteristics.

Accurate population estimates are dependent on satisfying the underlying assumptions. Assumptions essential for unbiased estimates of fish populations are probably seldom met to the degree necessary for obtaining useful data (Cooper, 1953). Therefore, it is necessary that invalid assumptions are understood so that data can be meaningfully interpreted. Assumptions necessary for indirect estimation of population size include:

- (1) mortality is equal between marked and unmarked fish
- (2) marks are not lost
- (3) population is closed - no significant migrations, recruitment, or death

- (4) either marked and unmarked fish are randomly distributed or sampling is randomized
- (5) fish do not learn to avoid capture gear
- (6) all fish are equally vulnerable to capture.

In short term population estimations studies, procedures can be designed to make assumptions (1), (2), and (3) readily acceptable. However, assumptions (4), (5), and (6) are often violated and probably contribute most to the estimation errors noted in many studies. Buck (1965) concluded that underestimation of fish populations was the result of vulnerability differences between marked and unmarked fish. He stated that differences in vulnerability could be the result of four factors:

- (1) failure of marked fish to redistribute randomly
- (2) greater susceptibility to capture due to marking
- (3) greater susceptibility to capture of certain individuals, independent of marks
- (4) ability to learn to avoid capture.

Ricker (1958) stated that it is extremely difficulty to evaluate effects of unequal vulnerability of marked and unmarked fish. This difficulty is probably reflected in the scarcity of investigations of this assumption in fisheries literature.

Accurate estimates of fish population size are essential to the intelligent management of most fishery resources and the understanding of population dynamics. However, accurate population estimates require an understanding of and an ability to compensate for all sources of

error. This study was designed to determine sources of systematic error in estimating fish populations and to compare commonly used capture gear and population estimators. Without knowing the causes of error, interpretation and improvement of population estimators cannot be accomplished. Increasingly complex estimators are of limited value unless we are familiar with the characteristics of the population being studied, know how well our assumptions are met, and can ultimately quantify those systematic errors encountered.

The study was conducted in Hoge Pond, a 1.16 hectare farm pond in Montgomery County, Virginia. Hoge Pond is fed by an intermittent stream which drains 0.82 square miles of pastureland. Characteristics of the drainage area probably contribute to the unusually high concentration of dissolved solids (220 ppm) and turbid conditions (visibility less than 0.7 m during study period). Nutrient loading from surrounding agricultural land also contributes to an abundance of filamentous green algae. Hoge Pond is relatively shallow with a maximum depth of 2.5 meters. Substrate is composed of fine silt and decomposing organic matter. Bottom sludge varies from one meter in depth at the inlet stream to 10 to 20 centimeters along much of the shoreline. Uniform substrate and a gradually sloping bottom provide ideal seining conditions. The outlet pipe, drainage pipe, several dock posts, and a partially submerged portion of dock were the only sampling obstructions.

METHODS

Preliminary samples collected with a 60-foot bag seine indicated that Hoge Pond contained pumpkinseeds (Lepomis gibbosus), bluegills (Lepomis macrochirus), and golden shiners (Notemigonus crysoleucas). Pumpkinseeds appeared to be the only fish species present in sufficient numbers to evaluate population estimators. Because seines and electroshockers are commonly used and have been shown to efficiently capture large samples of sunfish from small ponds (Hall, 1956; Bennett and Brown, 1968; Sandow, 1970), they were chosen for use in this study.

Only pumpkinseeds greater than 9.5 centimeters in length were included in the study. Fish smaller than 9.5 centimeters would have jeopardized objectives of the study due to excessively high mortalities caused by marking and being gilled by the seine. A 9.5 centimeter limit was chosen because it minimized the above problems and closely approximated a length frequency break. Exclusion of juvenile fish did not affect the experimental design or weaken conclusions. The study objectives required only the existence of a well defined population of fish.

The sampling schedule was designed to include two distinct sampling periods. The two sampling periods provided a marking and a recapturing period for single census estimates while permitting continuous marking and recapturing for estimating population size by multiple census methods. Depletion estimates could be calculated from data collected during either period. Each sampling period

consisted of alternating seining and electroshocking efforts in order to evaluate various collection methods.

Prior to sampling, the pond was divided into four quadrants (Figure 1). Each quadrant was further divided into five 100-foot sections of shoreline. The twenty 100-foot sections marked sampling stations for seining. A 60-foot, 3/8-inch mesh seine with a 6-foot bag was used. Seining was done by setting the net perpendicular to shore at one end of a 100-foot section. The seine was pulled perpendicular to shore and closed at the opposite end of the sampling section. By this method, all depths encountered could be effectively sampled although seining was confined to areas within 60 feet of shore.

On the first day of each sampling period, two seine hauls were made in each of the four quadrants. Fish were marked by appropriate finclip to indicate capture gear and sampling period, and by freeze-branding to indicate quadrant of capture. Freezebranding was done by anesthetizing fish with MS 222 and applying marks with branding irons cooled by liquid nitrogen. Fish were held until recovered then released at the center of the quadrant where captured. On all other seining days, six seine hauls were taken at randomly selected stations. Fish were marked by clipping half of the right pelvic fin during the first sampling period and by clipping the entire right pelvic fin during the second sampling period. All fish captured were measured to the nearest millimeter, examined for previous marks, and released at the site of capture. All seining was done between 1 pm and 5 pm in order to minimize effects of diurnal changes in fish distribution patterns.

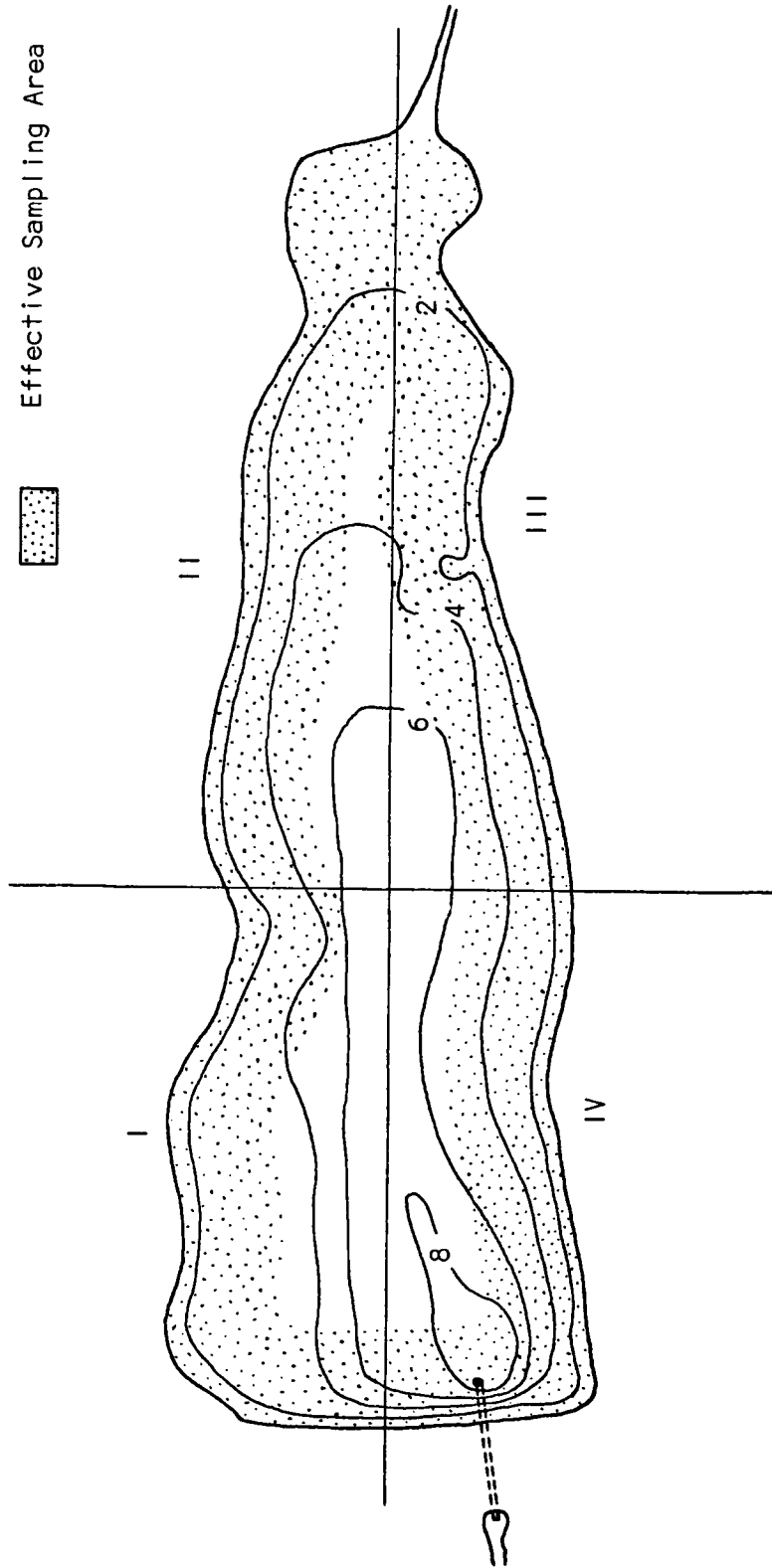


Figure 1. Topographical map of Hoge Pond indicating quadrants and effective sampling area.

Electroshocking was done with a variable output, DC shocking unit mounted in a fourteen-foot johnboat. Output was held constant at 120 pulses per second, 220 volts, and 4 amps of DC current. Initially, electrofishing was conducted in all areas of the pond. However, no fish were caught by electrofishing in deep water so subsequent sampling was done only near shore. A unit of sampling effort consisted of two passes around the pond perimeter. A single positive electrode mounted in front of the boat concentrated fish where they could easily be netted. Electroshocking was done immediately after dusk to standardize efforts and minimize effects of any possible diurnal changes in fish distribution patterns. All fish captured were held in live pens. During the first sampling period, fish were held until dawn before they were measured, examined for previous marks, and marked by clipping half of the left pelvic fin. During the second sampling period, fish were examined immediately following capture and marked by clipping the entire left pelvic fin. All fish captured by electroshocking were released at a single site near the center of the pond.

When recaptured fish represented approximately 40% of the total daily catch, Hoge Pond was drained to determine actual population size. A catch trap of hardware cloth was constructed below the outflow pipe to catch fish passing through the pipe. As the water level dropped, the pool remaining above the dam was seined. Seining was continued until less than 10 fish were caught per seine haul. The valve was then fully opened and the pond completely drained. The

exposed bottom and the small stream running through the pond were carefully searched for fish. No isolated pools remained and it was assumed that virtually all fish were recovered, measured, and examined for marks.

RESULTS

Population estimates based on mark and recapture methods are presented in Tables I and II. Single census estimates vary from 3759 to 4521 while multiple census estimates vary from 3039 to 3796. Single census estimates were consistently higher than multiple census estimates but differences were generally insignificant. Use of different sampling gear and different estimators had only minor effects on the estimates obtained. The small differences between estimates and relatively narrow confidence intervals suggests a fair degree of confidence in the results.

Population estimates based on catch per unit of effort data are presented in Table III. Without the opportunity to be compared with mark and recapture estimates, the depletion estimates would also appear consistent enough to be used for management purposes. However, comparison of mark and recapture and depletion estimates indicate that one or both methods of estimation produced severely biased results.

When Hoge Pond was drained, a total of 4141 pumpkinseed sunfish were recovered. This figure compares favorably with population estimates obtained by mark and recapture methods. However, only about 60% of the fish marked during the first sampling period and 70% of the fish marked during the second sampling period were recovered. Because escapement or loss of fish during drainage was considered negligible and a natural mortality rate of 40% over a six

Table 1. Estimated population size calculated by single census mark and recapture methods.

Marking Gear	Recapture Gear	Estimator ¹			
		Petersen		Schaefer	
		\hat{N}	C.I. ²	\hat{N}	C.I. ²
Seine	Seine	3914	3197;4631	3881	3174;4588
Electroshocker	Electroshocker	3780	3204;4356	3759	3189;4329
Electroshocker	Seine	4392	3393;5391	4335	3357;5313
Seine	Electroshocker	4521	3827;5215	4489	3804;5174
Seine and Electroshocker	Seine and Electroshocker	3791	3525;4057	3787	3522;4052

¹ Estimation models listed in Appendix.

² 95% confidence intervals, assuming a normal distribution.

Table 11. Estimated population size calculated by multiple census mark and recapture methods.

Marking Gear	Recapture Gear	Estimator ¹					
		Schnabel		Schumacher and Eschmeyer		Robson and Regier	
		\hat{N}	C.I. ²	\hat{N}	C.I. ²	\hat{N}	C.I. ²
Seine	Seine	3702	3169;4326	3550	3008;4092	3541	3061;4021
Electroshocker	Electroshocker	3048	2713;3425	3039	2703;3375	3167	2864;3470
Electroshocker	Seine	3346	2875;3895	3304	2569;4039	3406	2953;3859
Seine	Electroshocker	3743	3310;4233	3770	3335;4205	3796	3389;4203
Seine and Electroshocker	Seine and Electroshocker	3367	3142;3609	3342	3052;3632	3098	2947;3249

¹Estimation models listed in Appendix.

²95% confidence intervals, assuming a normal distribution.

Table III. Estimated population size calculated by catch per unit of effort data.

Sampling Gear	Sample Period	Number of Catches	Estimator ¹							
			DeLury		Seber & Le Cren ²		Robson & Regier ²		Zippin	
			\hat{N}	C.I. ³	\hat{N}	C.I. ³	\hat{N}	C.I. ³	\hat{N}	C.I. ³
Seine	First	5	1140	1013;1267	939	909;969	938	908;968	1243	1219;1267
Electroshocker	First	3	586	547;625	558	541;575	558	541;575	601	589;613
Seine	Second	6	440	404;476	500	247;753	498	245;751	492	449;535
Electroshocker	Second	6	948	904;992	557	363;751	557	363;751	1039	883;1195

¹ Estimation models listed in Appendix.

² Seber and Le Cren, and Robson and Regier models are for two catch data. The first two catches of each sampling period were used for calculation of population estimates.

³ 95% confidence interval, assuming a normal distribution.

week period seems unrealistic, losses were assumed to be due to mortality caused by handling and marking. If marking mortality is assumed to be the only cause of fish loss, actual population size at the beginning of the study would have been 4818. This figure is higher than all but 4 of 36 confidence intervals calculated from the study data.

An instantaneous rate of mortality was calculated from fish freezebranded on the first day of the second sampling period. When this mortality rate was applied to the entire marked population, the calculated mortality equaled the observed mortality. The number of marked fish in the population was adjusted by sampling day and population estimates were recalculated (Tables IV and V). After eliminating the positive bias associated with marking mortality, single census procedures underestimated the actual population size by an average of 34.1% and multiple census procedures by an average of 37.8%. Depletion estimators, although not biased by marking mortality, underestimated the actual population size by an average of 84.6% (Table III).

By completely draining Hoge Pond, the actual proportion of the population represented by a particular size class became known. It was, therefore, possible to evaluate size selectivity of the seine and electroshocker. Figures 2 and 3 illustrate size selectivity of each type of sampling gear. Graphs were formed by plotting the following relationship against each size class (data summarized in Appendix):

Table IV. Estimated population size calculated by single census mark and recapture methods from data adjusted for marking mortality¹.

Marking Gear	Recapture Gear	Estimator ²			
		Petersen		Schaefer	
		\hat{N}	C.I. ³	\hat{N}	C.I. ³
Seine	Seine	2848	2340;3356	2826	2412;3240
Electroshocker	Electroshocker	2968	2531;3405	2953	2519;3387
Electroshocker	Seine	3596	2788;4404	3551	2760;4342
Seine	Electroshocker	3215	2743;3687	3198	2731;3665
Seine and Electroshocker	Seine and Electroshocker	3281	3035;3527	2857	2672;3042

¹The number of marked fish in the population was determined by calculating a weighted average of the marked population during the entire recapture period. Actual population size at the beginning of the recapture period was approximately 4750.

²Estimation models listed in Appendix.

³95% confidence interval, assuming a normal distribution.

Table V. Estimated population size calculated by multiple census mark and recapture methods from data adjusted for marking mortality.

Marking Gear	Recapture Gear	Estimator ²					
		Schnabel		Schumacher and Eschmeyer		Robson and Regier	
		\hat{N}	C.I. ³	\hat{N}	C.I. ³	\hat{N}	C.I. ³
Seine	Seine	2893	2476;3381	2746	2270;3222	2533	2229;2837
Electroshocker	Electroshocker	2515	2238;2826	2453	2158;2872	2269	2092;2446
Electroshocker	Seine	2918	2507;3397	2844	2180;3508	3063	2650;3476
Seine	Electroshocker	2959	2617;3346	2937	2582;3292	3159	2807;3511
Seine and Electroshocker	Seine and Electroshocker	2676	2496;2868	2616	2354;2878	2721	2607;2835

¹Actual population size was estimated to average about 4480 during the study.

²Estimation models listed in Appendix.

³95% confidence interval, assuming a normal distribution.

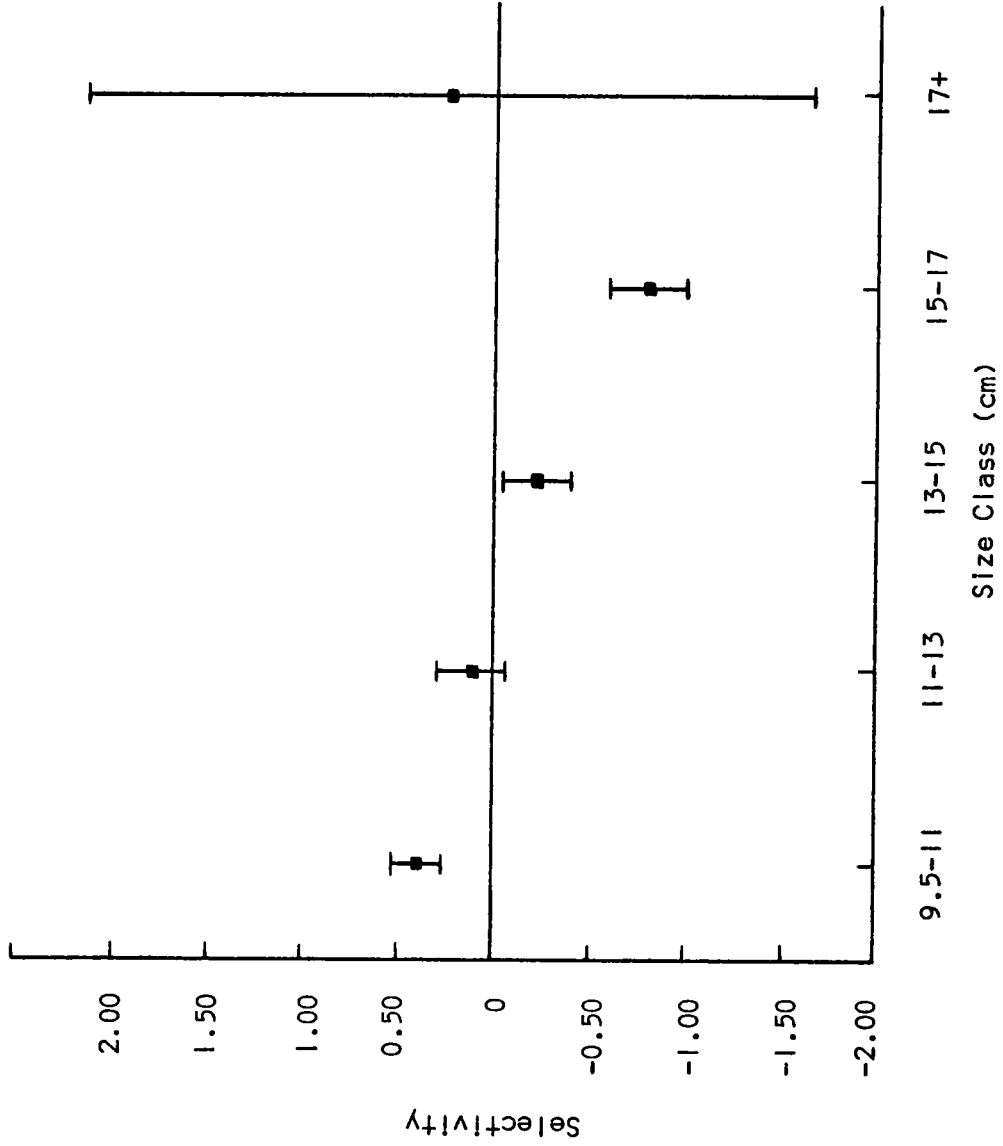


Figure 2. Size selectivity of a 60-foot bag seine used to collect pumpkinseed sunfish from Hoge Pond.

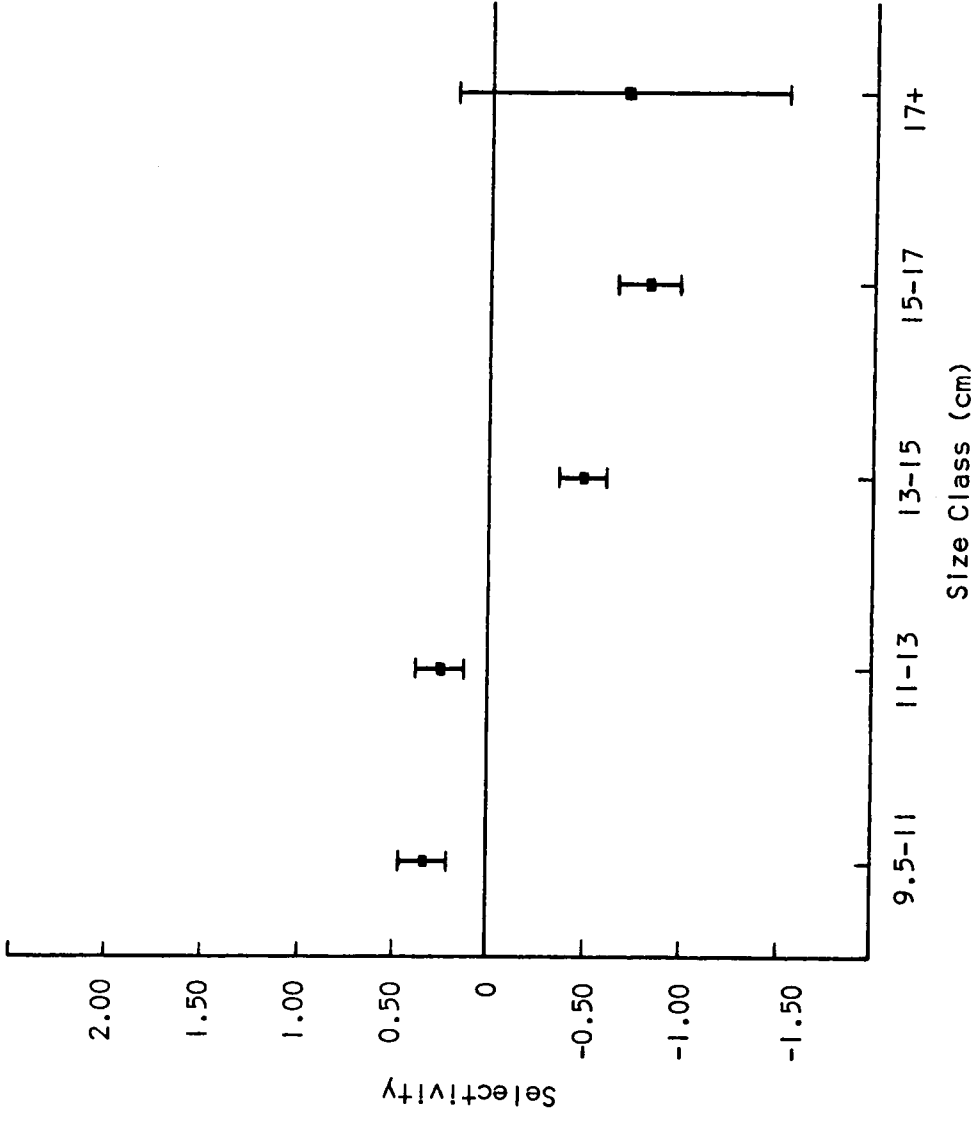


Figure 3. Size selectivity of electroshocking equipment used to collect pumpkinseed sunfish from Hoge Pond.

$$\frac{C_s/C_t - N_s/N_t}{N_s/N_t}$$

where: C_s = number of size (s) fish in catch

C_t = total catch at time (t)

N_s = number of size (s) fish in population

N_t = total population at time (t).

Confidence intervals were calculated by using binomial methods described by Dixon and Massey (1969). Both seining and electroshocking were found to be selective for smaller fish.

About 800 fish were marked by freezebranding to indicate site of capture. Area of recapture of freezebranded fish gave information on the redistribution of marked fish. Excessively high mortalities of fish freezebranded during the first sampling period greatly reduced the number of recaptures. Thirty-nine of 53 recaptures were caught in the same quadrants where originally marked (Table VI). Of 14 fish recaptured in other quadrants, 8 moved only the short distance between quadrants II and III (Figure 1). The remaining 6 fish moved between more widely spaced quadrants. The limited recapture results do not support the assumption of random redistribution of marked fish during this study.

Table VI. Redistribution of marked fish in Hoge Pond from quadrants where initially marked.

Quadrant Where Marked	Number Marked And Released	Quadrant of Recapture			
		Quadrant I	Quadrant II	Quadrant III	Quadrant IV
Quadrant I	71	6	0	0	0
Quadrant II	351	0	26	4	1
Quadrant III	205	0	4	3	2
Quadrant IV	135	1	1	1	4

DISCUSSION

The experimental design of this study followed procedures similar to those commonly used by fisheries investigators. When the study was planned, acceptance of underlying assumptions appeared relatively valid. During a short term study, there is usually little reason not to accept the assumptions that the population is closed, marks are not lost, and mortality differences are insignificant. Sampling could not be completely randomized due to the inefficiency of the sampling gear in deep water but, sampling was randomized within areas which could be effectively sampled. Lack of complete randomization was not considered a major problem because random mixing of marked fish appeared to be a reasonable assumption considering the small size of the pond. Randomization methods used in this study are commonly used and generally accepted procedures. Vulnerability differences between fish and ability of fish to learn to avoid capture gear are difficult factors to assess and are usually ignored by investigators. Within a limited size range, both vulnerability differences and learning are commonly assumed to be insignificant primarily on the basis that little evidence is available that challenges these assumptions. Although this type of reasoning may not be scientifically acceptable, it is often the only support available. Reasonable care was taken throughout the study to minimize sources of systematic errors attributable to the investigators. Despite using methods commonly used in lake and pond studies, and carefully executing described

procedures, all population estimates obtained were significantly biased.

Apparently, assumptions underlying population estimation procedures are often not met to the degree necessary to obtain reliable data and a more careful evaluation of these assumptions should be made before population estimation studies are initiated. It was evident from the results of this study that several of the underlying assumptions were not met. Mortality of marked fish was significant but the positive bias associated with marking mortality was not reflected in the estimates. Therefore, negative biases associated with other invalid assumptions must have compensated for the effects of mortality. Biases are probably the result of a number of systematic errors. In order to isolate individual sources of error, each assumption will be discussed in detail.

(1) Mortality is equal between marked and unmarked fish.

Equal mortality between marked and unmarked fish is an assumption which is often given little consideration when planning a population estimation study. Most investigators base their acceptance of this assumption on various studies which show no difference in mortality between marked and unmarked fish (Ricker, 1949; Shetter, 1951, 1952; Churchill, 1963). However, most marking mortality studies are not directly applicable to population estimation studies. When evaluating marking effects, both marked and unmarked (control) groups are handled and released. Effects of

stress due to handling are, therefore, reduced by the statistical design of marking mortality studies, but are not by the design of population estimation studies. Differential and natural mortalities are particularly given little consideration when population estimation studies are of short duration. Differences in mortality would be unimportant if total mortality was insignificant.

Results of this study indicate that marking mortality can be a major problem even in studies of short duration. Loss of marked fish could conceivably have been due to losses during drainage or natural mortality but both of these factors were considered unlikely. The assumption of marking mortality was supported by: (1) an observed poor health condition of many recaptured fish, (2) controlled efficiency of the drainage operation, (3) a greater return of fish marked later in the study, (4) no evidence of a large fish kill during the study, and (5) the low probability that natural mortality of fish larger than 9.5 centimeters could be 40% over such a short time period.

The exact causes of the mortalities in the marked population were not known. Effects of finclipping warmwater fish have not been studied in detail, but it is doubtful that removal of a pelvic fin would significantly reduce short term survival, particularly when predator density was as low as in Hoge Pond. It appears more likely that mortalities were the result of indirect factors relating to stress during the marking operation. This conclusion is supported by the fact that many recaptured fish had fungal and bacteria growths,

open sores, fin rot, and discoloration. Recaptures handled more than once were often in too poor a condition to be released. Stress due to handling has been shown to cause a number of physiological changes in fish (Stevens, 1972; Wedemeyer, 1972). With the poor health condition in Hoge Pond and the probable recent cessation of spawning, physiological stress caused by capture, handling, and marking could readily have increased the susceptibility of fish to parasites and disease.

Increased mortality of marked fish ultimately affects population estimates based on mark and recapture methods by decreasing the availability of the marked population and thus producing a positive bias. When estimating population size by depletion methods, however, marked fish are considered removed from the population and estimates are not affected by handling mortality.

In this study, if no other source of bias existed, handling mortalities would have resulted in a positive bias of 19.7% in single census mark and recapture estimates and 10.8% in multiple census mark and recapture estimates. Such biases could probably be significantly reduced with appropriate research but, at present, the magnitude of the problem in short term studies is not fully appreciated. Before population estimates can be considered valid, handling stress must be reduced to the point where fish are virtually unaffected.

Reduction of handling mortality alone is not sufficient to eliminate biases caused by handling. Mortality of marked fish produces a positive bias. Other compensating negative biases such as

increased susceptibility to capture can also be caused by handling. Elimination of handling stress to the point where it does not increase mortality or susceptibility of marked fish to capture must be accomplished. Handling stress can be reduced by minimizing handling of fish, and by planning studies for times when fish are not stressed by spawning, or environmental conditions. Mortality due to handling can also be reduced by not releasing recaptured fish. During this study, fish handled several times exhibited more advanced disease and parasite problems than fish handled only once. When evaluating underlying assumptions necessary for population estimation, effects of handling and marking must be carefully considered.

(2) Marks are not lost.

Marks can be lost by mortality of marked fish, by loss of the identifying mark, or by investigators failing to recognize marks. Loss of marks during this study was attributable only to mortality of marked fish. The pelvic finclips were easily recognized and did not regenerate over the short time period of the study. However, loss of marks in studies of longer duration could be a major problem. Fins will regenerate in time, tags are often lost, and loss of marks through natural and fishing mortality is difficult to assess. In short term mark and recapture studies, loss of marks other than through mortality can often be considered insignificant. For long term studies, a careful evaluation of marking procedures should be made on the particular species being studied. Marking procedures should be tested to insure a low percent loss of marks and the study should be

designed to permit assessment of losses through natural and fishing mortalities. If loss of marks cannot be estimated, population estimates cannot be adjusted for the positive biases that result.

(3) Population is closed.

A closed population implies no significant emigration, immigration, recruitment, or death. This assumption was probably adequately met in Hoge Pond. In short term studies, with juvenile fish excluded, recruitment and natural mortality can generally be assumed to be insignificant. However, if juvenile fish are included in the estimate, natural mortality could be a source of error. For estimating fish populations in ponds and small lakes, migrations probably are not a major problem. In large reservoirs and lotic situations, however, migrations can be a major source of error unless barriers exist. For very short term studies, sections of streams and coves can be blocked to eliminate migrations. On larger rivers and reservoirs migrations must be assumed to be negligible or migration rates must be estimated. A knowledge of a fish's behavior may provide justification for assuming no migrations. If migration, recruitment, or natural mortality cannot be considered negligible, a more advanced, complex estimator, which does not assume a closed population, must be used (Jolly, 1965; Seber, 1965). Use of these complex estimators require additional effort in collecting data but must be used if accurate estimates are to be obtained.

(4) Fish are randomly distributed or sampling is randomized.

Mark and recapture estimators are based on binomial statistics. Binomial statistics are applicable only if individuals are randomly captured from the population. Therefore, marked fish must be distributed randomly throughout the population or sampling must be randomized. Migratory and pelagic species may meet requirements of random distribution but considerable data suggests that most species restrict movements to a home range (Ball, 1947; Gerking, 1950; Hasler and Wisby, 1958; Shoemaker, 1952; Cooper, 1953; Miller, 1947; McLaren, 1970). If fish remain where originally marked, sampling efforts must be randomized. Many investigators use a system similar to that used in this study. Sampling stations are marked along the shoreline and sampling sites randomly selected. Randomization by this method randomizes efforts only within shoreline areas. Unless it can be assumed that marked fish distribute randomly between shore and offshore areas (which seems unlikely if it has been concluded that the species being studied restricts movements to a home range), sampling has not been completely randomized. In most population estimation studies conducted in large bodies of water, randomized sampling cannot easily be accomplished because of limitations of sampling equipment. Therefore, estimates obtained are negatively biased and represent only that portion of the population within areas which can be effectively sampled.

Results obtained by marking fish by quadrant of capture indicate that pumpkinseeds do not redistribute randomly. However, distances

between sampled and unsampled areas were short and some mixing may have occurred. As unsampled areas increase in size, biases associated with non-random mixing undoubtedly increase. Lack of randomization produces negative bias by concentrating marked fish in areas that can be effectively sampled. Because lack of randomization ultimately causes vulnerability differences between marked and unmarked fish, an evaluation of the magnitude of this error on the estimates obtained from Hoge Pond will be included in the discussion of vulnerability differences between fish.

Complete randomization of sampling efforts is difficult to achieve in many situations. Elimination of bias associated with lack of randomization will require use of sampling equipment capable of efficiently capturing fish from all habitat types.

(5) Fish do not learn to avoid capture gear.

Learning behavior is generally not well known prior to conducting a population estimation study because of a general lack of understanding of the learning abilities of fish. Depletion estimators are based on the assumption that fish do not learn to avoid capture. Any learned gear avoidance will reduce catchability and produce a negative bias in depletion estimates. Mark and recapture estimators are not affected by learning unless marked and unmarked fish learn at different rates. It could be argued that only fish captured (marked) have the opportunity to learn gear avoidance. However, most fish within a sampling area will be subjected to sampling efforts. Escapement

during initial efforts may be sufficient reward to cause fish to continue a flight response done initially by chance. It is also possible that a slight learning advantage, which would decrease catchability of marked fish, compensates for any increased catchability of marked fish due to individual behavioral, physiological, and anatomical characteristics. Increased catchability of marked fish associated with learning in mammalian studies is probably not a problem in fishery studies unless some type of baited capture gear is used.

In Hoge Pond, fish demonstrated a distinct ability to learn to avoid capture gear. Figures 4 and 5 illustrate the decrease in catch due to learning. Such a decrease could only be caused by learning, mortality, or seasonal redistribution of fish. Decreases in catch of this magnitude caused by mortality alone would have required approximately 60,000 dead fish over the first four sampling days. Such a fish kill could hardly go unnoticed nor would such mortalities seem realistic. Furthermore, if fish had died, catch per unit of effort could not have increased by suspending sampling operations for several days without significant recruitment (Figures 4 and 5). Data collected from freezebranded fish indicated that seasonal redistribution of fish had not occurred during the study. Few fish moved between the shallow water of quadrants II and III and the deep water of quadrants III and IV. Furthermore, redistribution of fish due to seasonal changes would not explain the sharp initial drop in catch and the increased catch after suspending sampling for

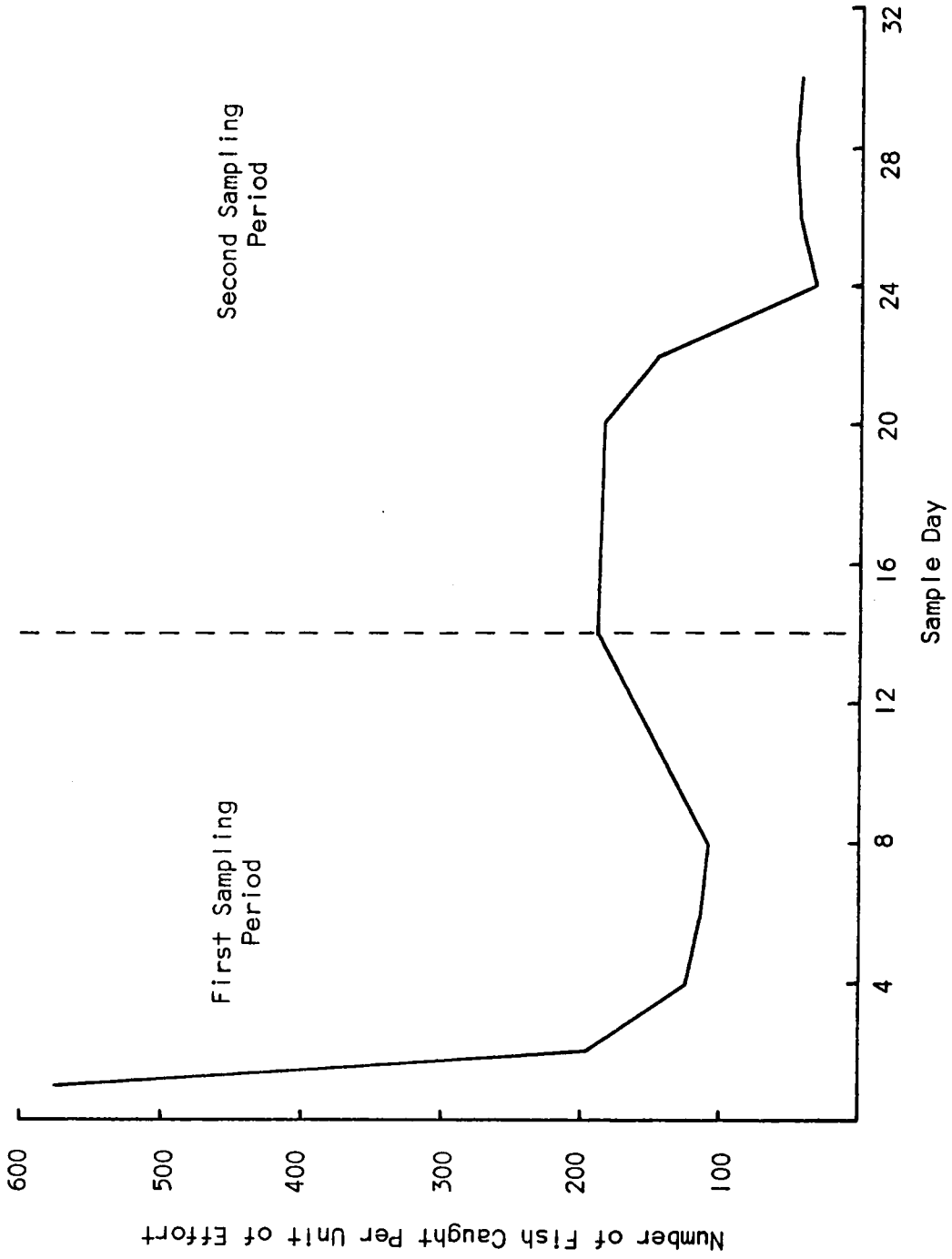


Figure 4. Changes in catch per unit of effort over time using a 60-foot seine in Hoge Pond.

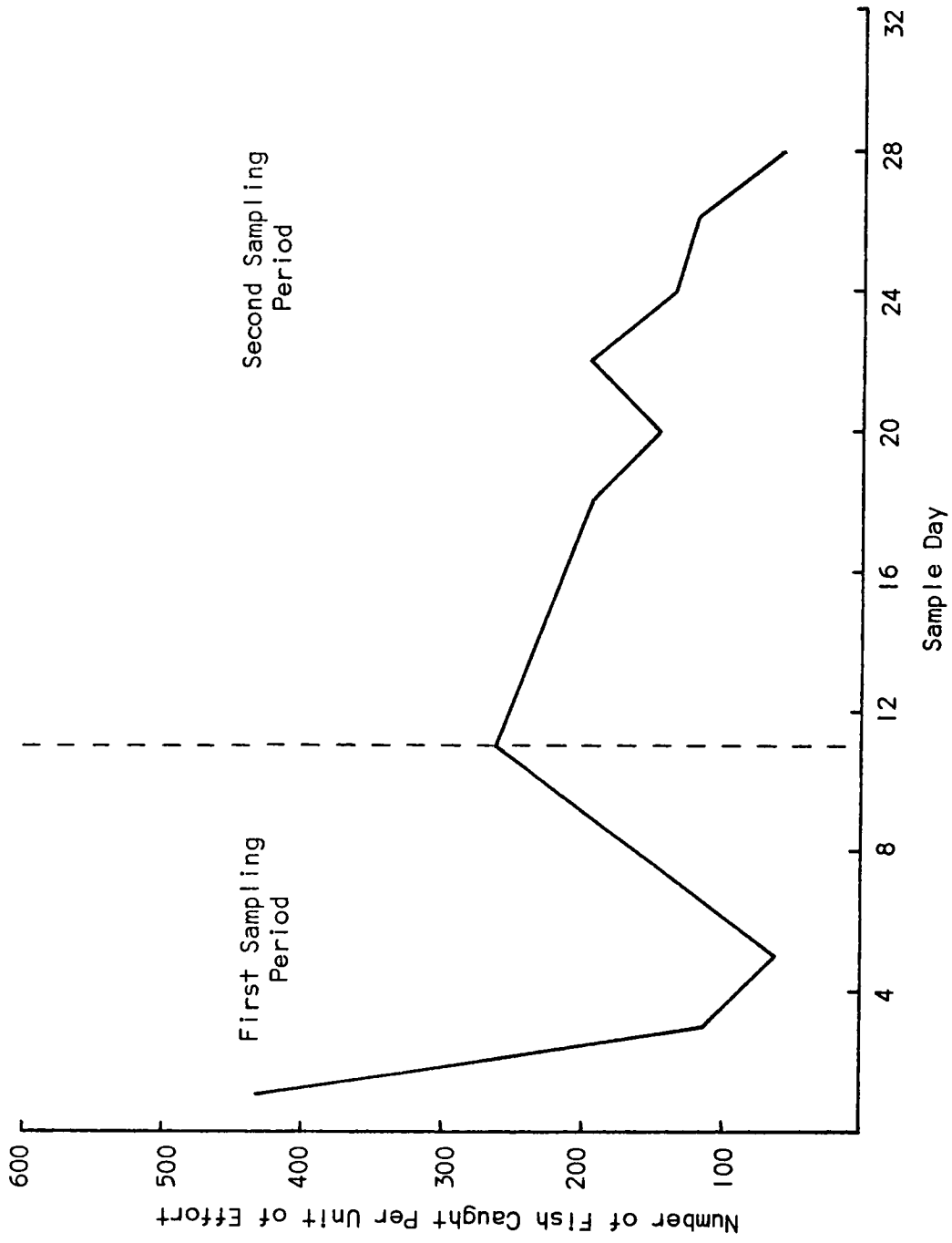


Figure 5. Change in catch per unit of effort over time using electroshocking equipment in Hoge Pond.

several days.

Ability of fish to learn to avoid capture gear makes management decisions based on depletion estimates questionable. Depletion estimators will usually be biased unless populations can be significantly reduced by a single unit of effort and opportunities for learning are minimal. Catch per unit of effort data on intensively fished commercial and sport fisheries may also be open to question. A decrease in catch per unit of effort may occur with little or no significant decrease in population size if fish learn to avoid capture. In such situations, decreasing exploitation by limiting catch would probably do little to benefit fishermen or fish populations. Conversely, periodic closures of the fishery could increase catch per unit of effort without an increase in population size if the extinguish rates for learned behavior and the length of the closure are comparable.

In this study, ability of fish to learn to avoid capture gear was probably the major source of bias associated with depletion estimators. However, bias associated with learning is confounded with biases associated with vulnerability differences between fish. Therefore, it is not possible to quantify effects of learning unless effects of vulnerability differences are known. A procedure for determining the amount of bias associated with both types of error is presented in the following section.

(6) All fish are equally vulnerable to capture.

Mark and recapture estimators are ultimately dependent on the assumption that marked fish are recaptured in proportion to their numbers in the population. A number of factors can cause differences in catchability of marked and unmarked fish. As mentioned above, distribution of fish can make marked fish more susceptible to capture by concentrating marked fish in areas which can be effectively sampled. Susceptibility of individual fish to capture may also vary due to behavioral, physiological, and anatomical characteristics. By marking more easily caught fish, the marked population becomes more susceptible to capture than the unmarked population. Another factor which may produce a negative bias is the effects of the marking operation. Handling stress and marking may decrease a fish's ability to avoid recapture. As discussed earlier, marked fish may have an increased opportunity for learning and learned avoidance may compensate for some negative biases. The assumption of equal vulnerability of marked and unmarked fish is the most important assumption to mark and recapture estimators but, because of the number and complexities of the factors involved, is poorly understood. All biases associated with mark and recapture estimators are ultimately caused by vulnerability differences between marked and unmarked fish.

Unbiased estimates of population size by mark and recapture methods is dependent on the accuracy of the following relationship:

$$r/C = m/N$$

where: r = number of recaptures

C = number of fish in the catch

m = number of marked fish in the population

N = total number of fish in the population

When data adjusted for handling mortality was tested by binomial methods (Dixon and Massey, 1969), it was found that r/C was significantly larger than m/N indicating that marked fish had a higher catchability than unmarked fish. The alpha level obtained (less than 0.001) leaves little doubt that inequalities observed in this study were the result of factors other than random error. Biases could be the result of a combination of factors. Because the biases are confounded, sources of error are not readily determinable. By developing several equations built around sources of systematic error, it is possible to describe sampling results. With a sufficient number of equations, unknowns (representing sources of error) can be calculated.

The following symbols will be used to identify changes in catchability which cause errors in population estimates:

Q = original catchability of the entire population

L = decrease in catchability of entire population

due to ability of fish to learn to avoid capture gear

H = increase in catchability of marked fish due to marks or handling

X = decrease in catchability of unmarked population due to elimination (marking) of more susceptible fish

X' = increase in catchability of marked fish due to segregation from harder to catch unmarked population.

X and X' are expressions of the same phenomenon. In order to decrease catchability of the larger unmarked population by a factor of X , catchability of the smaller marked population must be proportionately higher. X and X' do not affect catchability of the entire population, only catchabilities of the marked and unmarked populations when considered separately. X' can be expressed in terms of X by the following equation:

$$(1) \quad X' = ((N-m)/m)X$$

The number of recaptures on a particular sampling day can be expressed in terms of m , Q , L , X' , and H . Catchability of the marked population (m) is equal to the original catchability (Q), minus the decrease in catchability due to learning (L), plus the increase in catchability due to marking (H) and factors independent of marking (X').

$$(2) \quad r = m(Q-L+H+X')$$

Total daily catch can similarly be expressed in terms of N , m , Q , L , and H . Catchability of the entire population (N) is decreased

by learning (L) while catchability of the marked portion of the population is also increased by marking (H).

$$(3) \quad C = N(Q - L) + mH$$

The unmarked portion of the daily catch ($C - r$) can be expressed in terms of N , m , Q , L , and X . Catchability of the unmarked population ($N - m$) equals the original catchability (Q), minus the decrease in catchability due to learning (L), minus the decrease in catchability caused by marking more susceptible fish (X).

$$(4) \quad C - r = (Q - L - X)(N - m)$$

By method of substitution, the above equations can be solved for L :

$$L = \frac{Qm + Q + C - QN - r}{(m - N + 1)}$$

where: Q , m , C , N , and r are known values.

Values of L , X , X' , and H were calculated for each sampling day. The percentage contribution of each factor to the total bias observed in this study was then calculated and results summarized in Tables VII and VIII.

An overall learning ability (L) of the entire population does not bias mark and recapture estimates. Differential learning between marked and unmarked populations is included in X' along with biases

due to lack of randomization, size selectivity, and catchability differences between individuals. In this study, mark and recapture estimators were significantly biased only by an increased vulnerability of marked fish due to effects of marking (Table VII). Other biases included in X' may have been insignificant or may have acted in such a way as to cancel effects. Although illustrated in Figures 2 and 3, size selectivity did not significantly bias estimates. Mark and recapture estimates are not seriously biased by size selectivity if catchability within size classes remain constant. Bias due to size selectivity which may have occurred, may have been compensated for by higher handling mortalities within smaller size classes. Although not sources of bias in this study, other systematic errors associated with vulnerability differences which have been discussed may be responsible for bias in other studies.

The above analysis also showed that the depletion estimators were biased almost exclusively by the ability of fish to learn to avoid capture gear (Table VIII). Differences in catchability, including size selectivity, did not affect estimates because the proportion of the population removed was too small to significantly decrease catchability of remaining fish. If size selectivity is a significant source of error, populations can be estimated within size classes. However, this practice has the disadvantage of considerably decreasing precision.

Table VII. Percent contribution of catchability changes to the total negative bias of mark and recapture estimates obtained from Hoge Pond.

Marking Gear	Recapture Gear	L	H	X	X'
Seine	Seine	0	99.96%	0	0.04%
Electroshocker	Electroshocker	0	99.81%	0	0.19%
Electroshocker	Seine	0	99.61%	0	0.39%
Seine	Electroshocker	0	99.61%	0	0.39%

Table VIII. Percent contribution of catchability changes to the total negative bias of depletion estimates obtained from Hoge Pond.

Capture Gear	Sample Period	L	H	X	X'
Seine	First	-	-	-	-
Seine	Second	99.99%	0	0.01	0
Electroshocker	First	99.99%	0	0.01	0
Electroshocker	Second	99.99%	0	0.01	0

Choosing an estimator

The choice of which estimation procedure to use is dependent on the objectives of the study and whether or not certain assumptions can be supported. If assumptions cannot be adequately justified, an index of abundance may be just as valid and easier to obtain than a population estimate. Objectives such as calculating natural mortality, assessing results of management decisions, and determining conditions of fish populations can be accomplished with either procedure. Indices of abundance have the advantage of being less costly so that sampling efforts can be expanded and random errors reduced. However, population estimates, even without valid assumptions, permit the assessment of size and species selectivity of sampling gear. Where assumptions are not valid, management objectives could be effectively met by initially carrying out a population estimate to assess gear selectivity and by calculating an index of abundance in subsequent years. To make comparisons, sampling efforts must be constant from year to year and environmental conditions must be similar.

If all underlying assumptions can be met, population estimates will be accurate and the investigator should consider precision. Precision of depletion estimators is superior to that of mark and recapture estimators but situations where depletion estimators can be accurately used are limited. Unless the chances of escape are minimal, learning will probably bias depletion estimators. Precision of mark and recapture estimators is dependent on the percentage of the

population marked and the number of fish caught. Multiple census estimates are generally more precise than single census methods because they give the investigator the opportunity to be able to continue effort until a desired precision is reached. Single census methods are more susceptible to random error and the amount of effort necessary to obtain a desired precision is difficult to predetermine. Time, resources, and strength of underlying assumptions must be considered when choosing which type of procedure to use.

The choice of which estimation model to use is also a consideration. A number of models were compared in this study but none gave significantly more accurate results than the simple DeLury, Schnabel, and Petersen estimators. Theoretical biases of simpler estimators are insignificant if population size and number of recaptures are large. Furthermore, theoretical biases are generally positive and help compensate for negative biases commonly associated with systematic errors. Therefore, significantly increasing accuracy by using more advanced estimators is unlikely. The complex estimators which account for migrations, mortalities, and recruitment were not evaluated in this study but should be used if the population cannot be considered closed.

CONCLUSIONS

Population estimation studies are often carried out in situations where underlying assumptions cannot be adequately supported. So little concern is sometimes given to assumptions that it appears as though we believe that fish populations must comply to the "rule" which we have proclaimed. Underlying assumptions are generally accepted unless they can be proven wrong. This approach is not justified and may result in considerable loss of time and money. Before population estimates are made, an evaluation of assumptions should be carried out. If support of an assumption cannot be made, either a test of the assumption should be built into the study or the population estimates obtained should not be considered accurate.

Confidence intervals are often presented as a defense for the accuracy of a population estimate. Narrow confidence intervals seem to suggest confidence in the work of the investigator. However, confidence intervals are of no value if systematic errors are present. Confidence intervals provide a measure of random error and provide "confidence" in estimates only if underlying assumptions are valid. Precision should not be confused with or substituted for accuracy.

Results of this study indicate that effects of marking and learning may be the most serious causes of systematic error in estimating fish population size. Studies should be initiated to

determine the effects of handling stress and marking on fish catchability. By developing better marking and handling procedures, mark and recapture estimators could be significantly improved. Reduction of bias from depletion estimators may be more difficult. Learning can only be eliminated if sampling gear is efficient enough to make escape, except by chance, almost impossible. Such sampling devices may be difficult to design and could be uneconomical to build or operate.

Indiscriminate use of questionable population estimates is of little value to fisheries management. Without adequate support of assumptions, data collected are of limited use. Assumptions underlying population estimation procedures are not valid in many cases and should be given more careful consideration. The resources expended obtaining "population estimates" when assumptions cannot be supported, could probably be more useful expended on more meaningful investigations.

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APPENDIX

Table 1. Population estimation data collected by seining Hoge Pond.

Date	<u>Marked - Right Pelvic</u>		Catch	<u>Recaptures</u>		Released	Died ¹	
	<u>Unadjusted</u>	<u>Adjusted</u>		<u>Right Pelvic</u>	<u>Left Pelvic</u>			
	Half	Full	Half	Full	Half	Full		
9/19	67 ²	-	67	-	4	-	576 ³	0
9/20	67	-	63	-	1	-	187	3
9/22	251	-	228	-	5	12	112	0
9/24	363	-	319	-	8	6	103	5
9/26	461	-	408	-	13	20	86	0
10/2	547	-	455	-	37	16	141	7
10/8	681	-	520	-	27	30	174 ³	1
10/10	653	-	471	-	24	14	115	3
10/12	629	112	428	107	8	4	27	1
10/14	621	138	402	128	9	5	37	2
10/16	610	175	383	158	9	2	40	2
10/18	600	214	365	189	6	3	31	11

¹ Indicates number of marked fish which died between sampling days

² Fish marked during preliminary sampling.

³ Freezebranded fish were not included in the marked population because of high handling mortality.

Table 2. Population estimation data collected by electroshocking Hoge Pond.

Date	Marked - Left Pelvic			Catch	Recaptures			Released	Died ¹
	Unadjusted		Adjusted		Right Pelvic		Left Pelvic		
	Half	Full	Half		Full	Half	Full		
9/21	50 ²	-	45	431	26	-	2	239	3
9/23	286	-	264	113	3	-	14	85	0
9/25	321	-	332	63	9	-	9	49	2
10/2	368	-	332	262	53	-	30	219	1
10/9	586	-	477	192	30	-	34	174	0
10/11	552	174	424	142	18	8	11	117	0
10/13	541	291	396	194	33	13	21	147	2
10/15	519	437	366	136	16	9	19	103	0
10/17	500	540	339	122	14	9	18	88	1
10/19	482	627	316	57	4	9	10	0	0

¹ Indicates number of marked fish which died between sampling days.

² Fish marked during preliminary sampling.

Table 3. Data collected by draining Hoge Pond.

Length (cm)	Unmarked	Right Finclip		Left Finclip		Freezebrands		Double Marks ¹	Total
		Half	Full	Half	Full	9/19	10/2		
9.5-10	295	27	15	14	38	0	12	12	389
10-11	734	104	47	51	127	1	27	41	1050
11-12	509	46	27	59	69	1	13	29	695
12-13	308	44	32	52	79	3	22	49	491
13-14	289	39	19	46	45	4	19	31	430
14-15	544	53	20	47	59	12	7	20	722
15-16	239	14	5	23	9	8	3	9	292
16-17	48	2	-	3	-	-	-	-	53
17-18	3	-	-	-	-	-	-	-	3
18-19	2	1	-	2	1	-	1	2	5
19-20	4	1	1	2	1	1	-	1	9
20-21	2	-	-	-	-	-	-	-	2
Total	2977	331	166	299	428	30	104	194	4141

¹ Some fish marked several times. Numbers in this column must be subtracted from total.

Table 4. Size selectivity data collected by seining Hoge Pond.

Length (cm)	Sampling Day								Total Caught	Total in Population
	10/8	10/10	10/12	10/14	10/16	10/18	10/18	10/18		
9.5-10	25	27	7	7	13	5	5	84	377	
10-11	51	34	10	17	14	9	9	135	1022	
11-12	34	12	4	9	5	7	7	71	681	
12-13	30	18	5	2	3	8	8	66	466	
13-14	19	14	2	3	5	4	4	47	407	
14-15	12	11	3	2	1	6	6	35	703	
15-16	2	2	-	-	2	-	-	6	281	
16-17	-	-	-	-	-	-	-	-	53	
17-18	1	-	-	-	-	-	-	1	3	
18-19	-	-	-	1	-	-	-	1	4	
19-20	-	-	-	-	-	-	-	-	8	
20-21	-	-	-	-	-	-	-	-	2	
Total Catch	174	118	31	41	43	39	39	446	4007	

Table 5. Size selectivity data collected by electroshocking Hoge Pond.

Length (cm)	Sampling Day								Total Caught	Total in Population
	10/9	10/11	10/13	10/15	10/17	10/19	10/19	10/19		
9.5-10	21	34	38	18	26	5		142	377	
10-11	52	43	62	32	35	14		238	1022	
11-12	58	28	43	35	23	16		203	681	
12-13	26	10	21	14	8	7		86	466	
13-14	12	8	13	11	10	8		62	407	
14-15	8	7	7	9	9	1		41	703	
15-16	2	2	2	2	2	1		11	281	
16-17	-	-	-	-	-	1		1	53	
17-18	-	-	-	-	-	-		-	3	
18-19	1	-	-	-	-	-		1	4	
19-20	-	-	-	-	-	-		-	8	
20-21	-	-	-	-	-	-		-	2	
Total Catch	180	132	186	121	113	53		785	4007	

POPULATION ESTIMATION MODELS

I. Single census mark and recapture estimators

A. Petersen (1896)

(1) Estimator:

$$\hat{N} = \frac{mC}{r}$$

(2) Confidence Interval:

$$\text{S.E.}(\hat{N}) = \hat{N} \sqrt{\frac{(\hat{N} - m)(\hat{N} - C)}{mC(\hat{N} - 1)}}$$

B. Schaefer (1951)

(1) Estimator:

$$\hat{N} = \frac{(m + 1)(C + 1)}{(r + 1)}$$

(2) Confidence Interval:

Same as for Petersen

II. Multiple census mark and recapture estimators

A. Schnabel (1938)

(1) Estimator:

$$\hat{N} = \frac{\sum(m_i)(C_i)}{\sum r_i}$$

(2) Confidence Interval (Everhart, 1972):

$$r + 1.92 \pm 1.96 \sqrt{r + 1} = 95\% \text{ C.I. about } r$$

B. Schumacher and Eschmeyer (1943)

(1) Estimator:

$$\hat{N} = \frac{\sum (m_i)^2 (C_i)}{\sum (r_i)^2 (m_i)}$$

(2) Confidence Interval:

$$s^2 = \frac{1}{k-1} \left[\sum \left(\frac{r_i^2}{C_i} \right) - \frac{1}{N} \sum (mr) \right]$$

$$S.E.(\hat{N}) = \hat{N} \sqrt{\frac{\hat{N}s^2}{\sum mr}}$$

C. Maximum Likelihood Method (Robson and Regier, 1971)

(1) Estimator:

$$P_{\hat{N}}(1, \dots, k) = \frac{\hat{N} - U_k}{\hat{N}}$$

where:

$$P_{\hat{N}}(1, \dots, k) = \pi \left(\frac{\hat{N} - B_i - C_{i+1}}{\hat{N} - B_i} \right)$$

U_k = total number of unmarked fish caught in
k samples

B = number of fish removed from the population

(2) Confidence Interval:

$$S.E.(\hat{N}) = \sqrt{\frac{\hat{N} - U}{\Delta \hat{N}}}$$

where:

$$\Delta \hat{N} = 1 + (\hat{N} - 1) P_{\hat{N}} - NP_{\hat{N}}$$

D. Maximum Likelihood Method - different capture and recapture gear. (Robson and Regier, 1971)

(1) Estimator:

$$\pi\left(\frac{\hat{N} - B_i - m_i - C_i - r_i}{\hat{N} - B_i - m_i}\right) = \pi\left(\frac{\hat{N} - B_i - C_i}{\hat{N} - B_i}\right)$$

where: B = number of fish removed from the population.

(2) Confidence Interval:

$$S.E.(\hat{N}) = \frac{\hat{N} - B_i}{\sqrt{(\hat{N} - B_i - 1) \Sigma \left[\frac{C_i + m_i}{(\hat{N} - B_i - m_i)(\hat{N} - B_i - C_i)} \right]}}$$

III. Depletion Estimators

A. Delury (1947) - Linear Regression

(1) Estimator:

Catch is plotted against previous accumulated catch. A least squares line is fitted to the data points and the estimated population size is that point where the line crosses the X-axis.

(2) Confidence Interval:

Calculated by determining the standard error of the least squares line.

B. Seber and Le Cren (1967)

(1) Estimator:

$$\hat{N} = \frac{(C_1)^2}{(C_1 - C_2)}$$

(2) Confidence Interval:

$$\text{S.E.}(\hat{N}) = \frac{C_1 C_2}{(C_1 - C_2)^2} \sqrt{C_1 + C_2}$$

C. Robson and Regier (1971)

(1) Estimator:

$$\hat{N} = \frac{(C_1)^2 - C_2}{C_1 - C_2}$$

(2) Confidence Interval:

Same as for Seber and Le Cren

D. Zippin (1958)

(1) Estimator:

$$\hat{N} = \frac{T}{1 - \hat{q}_k}$$

where: T = total catch

$1 - \hat{q}_k$ = estimated proportion of the population
captured - from graph (Zippin, 1958)

(2) Confidence Interval:

$$\text{S.E.}(\hat{N}) = \sqrt{\frac{\hat{N}(\hat{N} - T)T}{T^2 - \hat{N}(\hat{N} - T) \frac{(k\hat{p})^2}{1 - \hat{p}}}}$$

where: \hat{p} = estimate of the probability of capture during
trapping - from graph (Zippin, 1958).

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AN EVALUATION OF SYSTEMATIC ERROR IN THE
ESTIMATION OF FISH POPULATION SIZE

by

Larry O. Mohn

(ABSTRACT)

Various estimation models and numerous sampling methods were used to estimate the size of a pumpkinseed sunfish (Lepomis gibbosus) population in a 1.16 hectare Virginia farm pond. After estimates were obtained, the pond was drained in order to compare estimated population size with actual population size.

In all cases, population estimates were significantly less than actual population size. An examination of the underlying assumptions indicated that biases were attributed to mortality of marked fish, an increased catchability of marked fish due to marking, and the ability of fish to learn to avoid capture gear. Different gear combinations and use of different estimation models had no significant effect on the accuracy of estimates obtained.

The study was designed to employ commonly used methods of estimating population size in a situation where underlying assumptions appeared relatively valid. It is apparent from the results of this study that underlying assumptions are often not met to the degree necessary to provide useful data.