

THE UNIVERSITY OF MANITOBA

Evaluation of the Effects of Fry and Fingerling
Plants on Walleye, *Stizostedion vitreum vitreum*
(Mitchill), Production in West Blue Lake,
Manitoba *via* Isozymes of Malate Dehydrogenase

by

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JACOB F. SCHWEIGERT

A dissertation submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

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ABSTRACT

The axiom that fish stocking is an effective and beneficial management concept was quantitatively examined by employing unique isozyme phenotypes of the enzyme malate dehydrogenase in skeletal muscle as biological markers. Walleye fry plants in the spring of 1971 and 1972 and a fingerling plant in the fall of 1972 were monitored in monthly gillnet samples by starch-gel electrophoresis to determine their relative survival, contribution to the year-classes, and effects on production of the native walleye population. The 1971 fry plant augmented the year-class by 43% but averaged only 2.2% of the total catch during 1974-1975. In contrast, the 1972 fry and fingerling plants comprised the entire year-class (98.5%) and contributed 35.5% of the total catch in 1974-1975. The fingerling plant was marginally successful contributing only 7.75% to 1972 year-class abundance. Annual population production was 341 kg from August 1974-August 1975. The introduced fish contributed the majority of this production (51.5%) of which the 1972 fry introduction comprised 95%. The 1971 fry and 1972 fingerling introductions contributed equally to the remainder - about 1% of total annual population production. Fry planting is preferential to fingerling plants as a

means of increasing population production. The isozyme marking system is virtually flawless and deserves consideration in other suitable population dynamics studies.

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INTRODUCTION

The artificial propagation and augmentation of depleted fish stocks is a widely practiced and generally accepted management technique. The efficacy and practicality of this approach has seldom been examined. Studies designed to evaluate and remedy the drastic declines in freshwater and marine fish stocks uniformly ignored artificial propagation (Parrish 1973, Roedel 1975, Loftus and Regier 1972, Regier, *et al.* 1969) as a possible solution. This results, in part, from pessimism regarding early studies (Dymond 1957) which generally attempted to correlate numbers of fry planted with the resultant year-class strengths from catches in commercially exploited populations in large water bodies but failed to illuminate the nature of any such relationship (Hile 1937, Carlander 1945, Smith and Krefting 1954). Recent studies based on alternate- or multi-year stocking strategies (Rose 1955, Forney 1975, 1976, Carlander, *et al.* 1960) indicate apparent enhancement of some augmented year-classes probably the result of higher stocking densities.

The major obstacle to a quantitative evaluation of fish stocking is the inability to distinguish introduced from native fish once the two groups have intermingled. Previous studies all suffer from the

necessity of attributing apparent changes in year-class strengths directly to the fry plants without prior knowledge of population structure and dynamics.

The objectives of the present study are

(1) to evaluate the viability of malate dehydrogenase (MDH) isozyme phenotypes as distinctive biological markers for application in fish introduction and other population dynamics studies, (2) employ the MDH marking system to quantify the effects of fry and fingerling plants on year-class strength and production of the native walleye (*Stizostedion vitreum vitreum*) population and evaluate their rationale as a sound management practice in increasing production of exploited and unexploited fish populations.

Recently, Clayton, *et al.* (1971) found that the walleye possesses six possible isozyme phenotypes for the enzyme malate dehydrogenase in skeletal muscle. The heritability of the phenotypes is explicable by simple Mendelian genetics permitting accurate prediction of the egg and fry phenotypes (Clayton, *et al.* 1971) to be employed in an introduction. The allele designated C¹ is apparently restricted to a small number of water bodies in the Churchill River system (Clayton, *et al.* 1974). This facilitates the interbreeding requisite to obtaining uniquely identifiable offspring.

The small closed system environment of West Blue Lake with the lack of major predator species and the virtual absence of the C^1 allele provided an ideal situation in which to monitor and assess the success of fry and fingerling plants bearing the distinctive C^1 allele as a biological "mark". In addition, considerable background information is available on year-class strengths, growth, and seasonal changes in biomass and production of the native walleye population providing a comprehensive standard against which to assess the effects of the fry and fingerling plants (Glenn 1969, Kelso and Ward 1972).

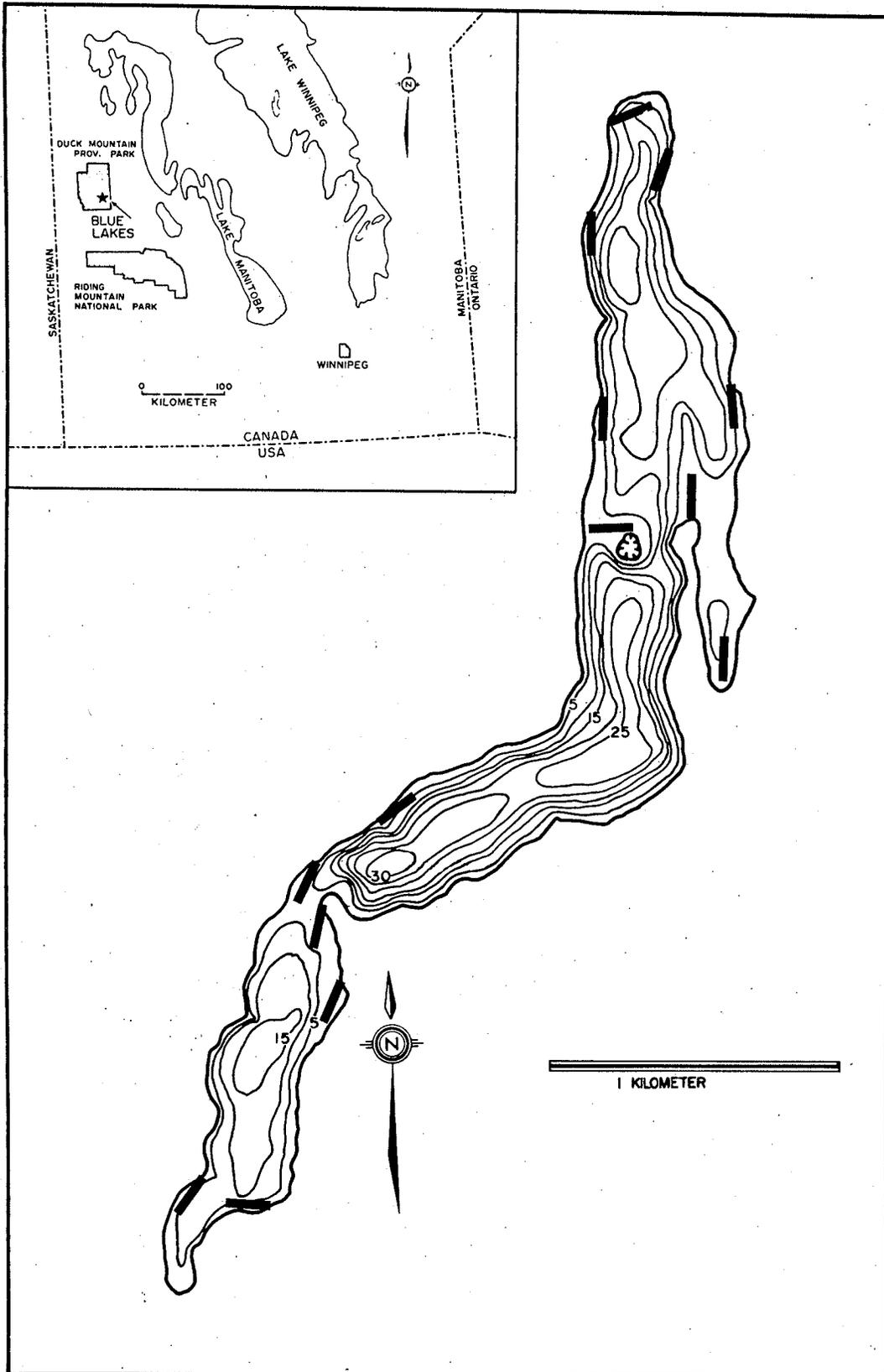
Initial monitoring suggests that the small walleye fry plant in 1971 was moderately successful while the larger plant in 1972 introduced a complete, abundant artificial year-class (Ward and Clayton 1975). Monitoring was continued to confirm initial findings, to examine the long term viability of the marking system as well as differential mortality of stocked fry, and to evaluate the potential contribution of fry and fingerling plants to the harvestable walleye stock and production in West Blue Lake.

MATERIALS AND METHODS

West Blue Lake is located in Duck Mountain Provincial Park, approximately 500 km northwest of Winnipeg, Manitoba (Fig. 1). The lake is long, narrow, and steep-sided with three main basins. The maximum length is 4.8 km, maximum depth 31m, and mean depth 11.3 m. Area is 160 ha (Bell and Ward 1970). There is no outlet stream and only two small temporary inlet streams draining swamp to the west. Ice cover usually forms in mid-November, reaches a maximum thickness of about 1 m in early spring, and leaves in mid-May. During the ice-free period Secchi disc transparency varies between 5 and 10 m. Thermal stratification occurs in late May or early June. Dissolved oxygen levels remain high above 15 m during most of the open period, but is depleted in regions deeper than 20 m during the summer. Meromixis is present in some years. Total alkalinity as CaCO_3 approximates 150 mg/l during summer when epilimnion pH ranges from 8.0 to 8.6 and that of the hypolimnion from 7.0 to 8.0 (Ward and Robinson 1974).

The parental walleye stock used to provide fry for the West Blue Lake plants overwinter in Crean Lake, Prince Albert National Park, moving into adjacent streams to spawn in spring. Pre-spawning fish were trapped in a tributary of Crean Lake and retained in pens until ripe.

Figure 1. A contour map of West Blue Lake and its location in Manitoba, indicating the main gill netting sites, (depth in meters).



In early May 1971, thirty-six 1 x 1 matings were made and fertilized eggs were held at the spawning site. Spawned fish were killed and the MDH phenotypes of each individual determined. Egg lots representing matings of the type C^1C^1 x C^1C^1 and C^1C^1 x C^1C^3 were selected for the subsequent fry plant into West Blue Lake and were incubated in a small field hatchery. In late May the eggs were transferred to the provincial hatchery at Duck Bay, Manitoba and 50,000 to 100,000 resultant fry released into West Blue Lake on June 1.

In 1972 the phenotypes of adult fish were determined prior to spawning and only matings of the type C^1C^1 x C^1C^3 were made. The desired matings were made during the period May 7 to 13 using groups of four to six fish. Eggs were transferred to the provincial hatchery at Fort Qu'Appelle, Saskatchewan, for incubation. On May 26 they were transferred to a small field hatchery at West Blue Lake and incubated until hatching was complete on June 4. On June 6 fry were photographed and 373,000 were released at various locations on the lake (Ward and Clayton 1975). Another 186,000 fry were transferred to small ponds at Erikson and 2,500 fin-clipped fingerlings subsequently planted into West Blue Lake in the fall of 1972.

During the summer of 1972 and 1973 small mesh (1.9 cm, stretched measure) gill nets were used to sample small walleye for MDH analysis (Ward and Clayton 1975).

Sampling procedures for population enumeration during the years 1972 to 1975 consisted of capturing fish in a standard gang of gill nets composed of three sections each 30.5 m long and 1.8 m deep. Mesh sizes were 3.81, 6.35, and 8.89 cm stretched measure (Kelso and Ward 1972). The nets were set between 2000 and 2200 hrs, angularly to shore and usually in less than 5 m of water (Fig. 1). The nets were checked for fish at 20 - 30 minute intervals, more frequently if the catch was heavy. During 1972-1974, 2 gangs were fished each day of sampling and in 1975 2 - 4 gangs were fished depending on available manpower. Fish were removed from the nets as soon as possible after capture and placed in a 25 l container of water. Fish were then transferred to a "live box" where they were retained overnight (Kelso and Ward 1972).

Fish were separated by the mesh size of capture beginning in August 1974. The next morning fish were examined for condition, total and fork lengths measured, and scale samples were taken from the left side above the lateral line between the two

dorsal fins. Floy FD-67 individually numbered anchor tags (Dell 1968) were inserted in the back below the middle of the first dorsal fin. During the summer of 1975 two tags were applied, one on either side, to assess tag loss.

Tissue biopsies for isozyme phenotype determinations were also taken from some fish. In addition to the fish sacrificed from small mesh catches during 1972 and 1973, 10% of the standard gang catch in 1973 was sacrificed for MDH analysis. In May 1974 the hypodermic syringe described by Uthe (1971) was tested as a means of obtaining tissue samples without sacrificing fish. Concomitant with the first three mark and recapture periods of 1974 control and biopsied fish were held in 560 l tanks on the lakeshore to assess mortality attendant to capture and handling. Beginning in June 1974 the hypodermic syringe was used exclusively to obtain tissue biopsies from every second fish in 1974 and every fifth individual from standard gang catches in 1975.

The actual MDH isozyme phenotypes were determined *via* starch-gel electrophoresis. Tissue samples were prepared for electrophoresis by homogenization of white muscle tissue with a distilled water solution of nicotinamide adenine

dinucleotide (NAD) 300 mg/l, in a Teflon and glass tissue grinder. Syringe muscle samples were ground by hand using a glass stirring rod. Extracts were prepared from the white muscle in the ratio 1 gm tissue/2 ml extraction solution and clarified by centrifugation at 25,000 g and 2°C. Starch-gel electrophoresis (Tris-citrate buffer pH 8.0) and isozyme visualization was carried out as described by Clayton and Gee (1969) with the substitution of malic acid for lactic acid in the present study (Clayton, *et al.* 1971).

A total of seventeen mark and recapture samplings were conducted from 1972 through 1975 at approximately one month intervals over the summer except in July when water temperatures were above 20°C. Population abundances were determined for all periods by both the Chapman (1952) single release, and Jolly-Seber multiple release procedures (Cormack 1968). The former estimates were adjusted for tag loss following Cucin and Regier (1965). Recruitment and survival estimates are implicit in the approach of Jolly (1965), which was modified to adjust for small sample bias (Seber 1973). The no-birth model of Jolly (1965) again modified for small sample bias was applied to the 1972 year-class for the period August 1974 through September 1975. The catch

curve method of Robson and Chapman (1961) provided an estimate of annual mortality for comparison with estimates by Jolly's model. The procedure outlined by Robson (1969) was followed to test for mortality attendant to sampling and marking.

Growth rates were determined both directly from lengths and indirectly from scales. Instantaneous daily rates of growth in length (g_L) were determined directly from:

$$g_L = \frac{\log_e l_2 - \log_e l_1}{t_2 - t_1}, \text{ where } l_i \text{ is length at time } i$$

(Ricker 1975). Lengths were converted to weight using the relationship $.000003443 \log_e^{3.163}$ (Glenn 1969). To compensate for negative growth rates resulting from small sample size for some year-classes weighted linear regression was applied to weights for seasonal growth estimates in 1974 and 1975 (Steel and Torrie 1960).

To determine population growth indirectly from scales, acetate impressions were magnified 46.5 times using a bioscope and the distance to each annulus and the scale radius were measured to the nearest millimeter in the anterior field. All scales were read twice, disagreement resulting in further reading. Only scales meeting the criteria of Hile (1954) were used for determining growth. Of the 2,523 fish captured over the four years 2,437 individuals could be used for growth

studies. The last week of June (Glenn 1969) was taken as the time of annulus formation unless an annulus was obviously present in assigning fish to brood years.

A power function was fitted to the scale radius-total length relationship (Hile 1941) to back-calculate lengths at previous annuli. In each case an estimated scale radius was determined for each fish from the relationship for the particular year using its total length and this theoretical length was compared to the actual measured length to provide a correction factor to each measured annulus on that individual. The distances between annuli, ΔL_i were obtained by subtraction. Seasonal growth rate relative to the last annulus was obtained from:

$$h = \frac{S_{i+1} - S_i}{S_i} \quad \text{where } h = \text{relative growth rate}$$

$S_i = \text{size at time } i$

The relative growth rates (h) were transformed to instantaneous rates (g) by the relationship $g = \log_e (h + 1)$.

The combination of abundance estimates and mean weight of each year-class permitted the estimation of biomass at six sampling times during 1974 and 1975, where biomass consists of the 1966-1973 year-classes. Average biomass (\bar{B}) of the stock was the arithmetic

mean of adjacent biomass estimates (Chapman 1968) and production was calculated using the Chapman modification of the Ricker (1946) approach, $P = g\bar{B}$, where g is the instantaneous growth in weight.

Production of introduced fish was apportioned on the basis of their per cent frequency in the population as estimated by the relative proportions of native and introduced fish in the isozyme determinations. Production of the strong 1967 and 1972 year-classes was also determined by the graphical approach (Allen 1951). The population estimates and mean weight were used directly and also by fitting a curve to abundance estimates (Chapman 1968), to obtain production. The 1972 year-class was subdivided into Erikson and introduced fish based on the frequency of the former in catches during 1974 and 1975 and the latter from isozyme phenotype data and production determined by Chapman's arithmetic procedure.

RESULTS

I Releases

The introduction of 50,000 to 100,000 walleye fry bearing the C^1 allele into West Blue Lake in 1971 resulted from 1.1×10^6 eggs produced by mating $C^1C^1 \times C^1C^1$ and $C^1C^1 \times C^1C^3$ parents at Crean Lake (Ward and Clayton 1975). Similarly, $C^1C^1 \times C^1C^3$ matings at Crean Lake in 1972 provided 4.5×10^6 eggs from which 2.0×10^6 viable eggs reached West Blue Lake and resulted in 560,000 fry of which 373,000 were released into West Blue Lake. The remaining 187,000 fry were planted in ponds at Erikson, Manitoba and provided 2,500 fingerlings for a small planting in October 1972.

II Sampling and Analyses of Catches

The contribution of these introductions relative to both the native year-classes and the population as a whole was monitored by examining their frequency in samples taken by the standard gill net gangs (Table 1).

Age determination permitted the assessment of relative year-class strengths and their proportions in the population. Year-class strengths fluctuate

Table 1. Age- and percentage-frequency of walleye year-classes in the standard gillnet gang catches seasonally and annually for 1972-1975.

Year Class	1972							1973						
	May 17-31	June -24 July 2	July 18-26	Sept. 13-19	Total	%	May 16-23	June 12-19	July 9-19	Aug. 20-25	Sept. 10-17	Total	%	
1963	3	0	0	0	3	0.8	0	0	0	0	0	0	-	
1964	3	2	0	0	5	1.3	2	0	0	0	0	2	0.4	
1965	3	0	0	1	4	1.1	1	4	1	1	0	7	1.3	
1966	4	0	1	2	7	1.9	8	10	4	9	3	34	6.2	
1967	125	72	28	107	332	87.8	89	73	93	103	81	439	80.4	
1968	0	2	0	2	4	1.1	1	0	0	3	2	6	1.1	
1969	2	1	1	5	9	2.4	1	3	4	4	5	17	3.1	
1970	1	1	0	10	12	3.2	5	3	9	8	4	29	5.3	
1971	1	0	1	0	2	0.5	3	1	1	1	5	11	2.0	
1972	-	-	-	-	-	-	-	-	-	1	0	1	0.2	
1973	-	-	-	-	-	-	-	-	-	-	-	-	-	
1974	-	-	-	-	-	-	-	-	-	-	-	-	-	
Total	142	78	31	127	378		110	94	112	130	100	546		

TABLE 1 CONT'D ON NEXT PAGE

Table 1. Age- and percentage-frequency of walleye year-classes in the standard gillnet gang catches seasonally and annually for 1972-1975.

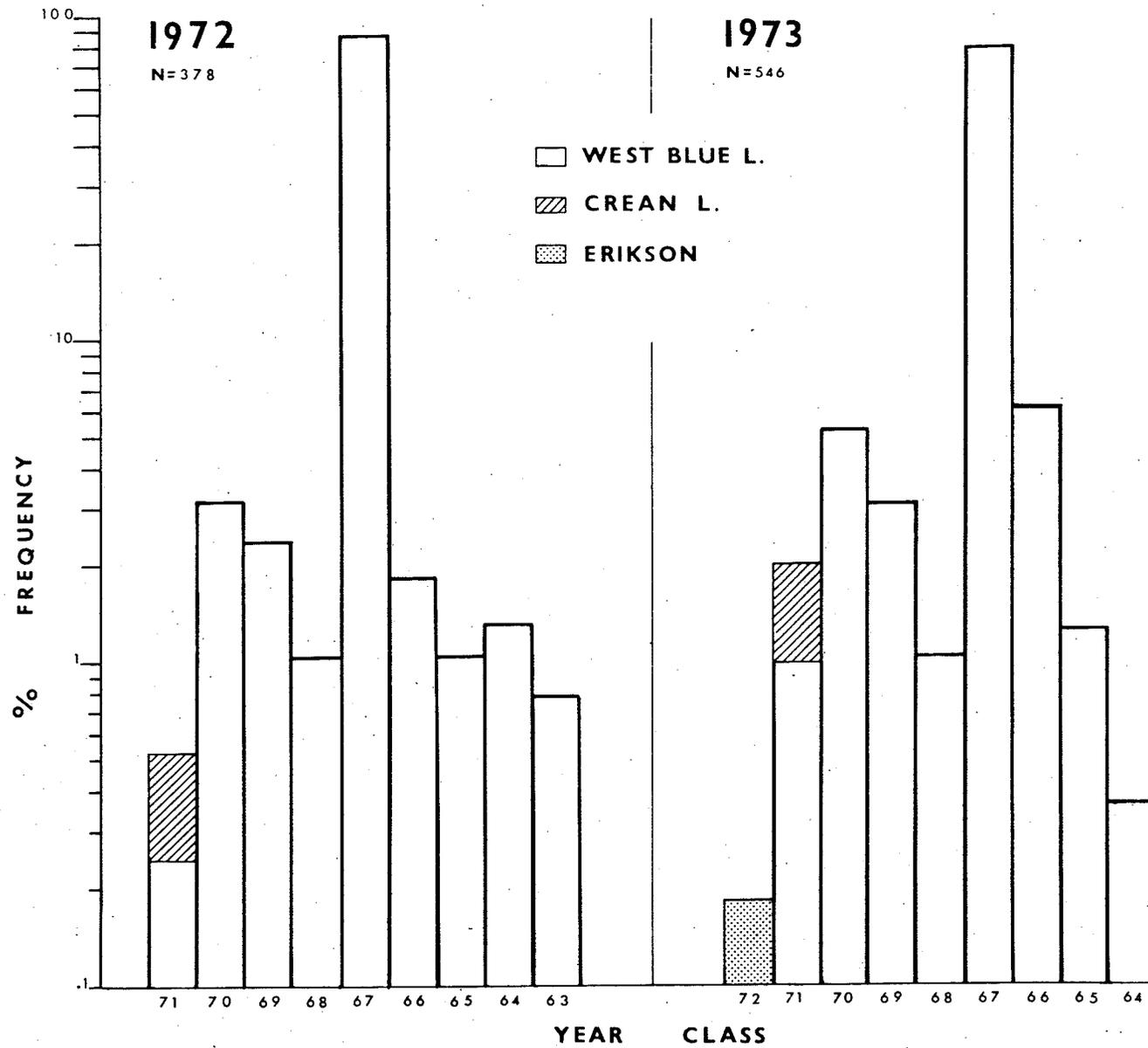
Year Class	1974						1975					
	May 21-31	June 17-21	Aug. 13-18	Sept. 14-17	Total	%	May 15-20	June 15-19	Aug. 5-11	Sept. 2-6	Total	%
1963	0	0	0	0	0	-	0	0	0	0	0	-
1964	0	0	0	0	0	-	0	0	0	0	0	-
1965	2	0	0	0	2	0.4	1	0	0	0	1	0.1
1966	6	3	5	4	18	3.8	16	7	4	2	29	3.2
1967	90	68	54	46	258	54.7	166	131	59	87	443	48.4
1968	1	0	1	2	4	0.8	1	2	2	1	6	0.7
1969	0	3	2	2	7	1.5	8	5	2	3	18	2.0
1970	1	3	1	1	6	1.3	2	4	2	2	10	1.1
1971	4	8	1	2	15	3.2	1	6	3	1	11	1.2
1972	14	70	37	35	156	33.1	31	103	126	87	347	37.9
1973	-	-	3	3	6	1.3	0	6	12	11	29	3.2
1974	-	-	-	-	-	-	-	-	16	6	22	2.4
Total	118	155	104	95	472		226	264	226	200	916	

markedly (Table 1) as noted by the age frequency distribution in Figure 2. Particularly abundant are the native 1967 and the introduced 1972 year-classes. Also apparent are the relative rates and magnitude of recruitment and mortality, the former occurring primarily during the second year and the latter becoming pronounced after the 8th year of life (Fig. 2).

Since the year-classes augmented by introductions in 1971 and 1972, would not be recruited into standard gang catches until 1973 and 1974, respectively, samples for isozyme analysis were obtained with small mesh gill nets (Table 2) to determine relative proportions of the native and introduced fish in these year-classes during 1972 and 1973. The 1971 year-class was found to consist of 52.6% introduced fish in 1972 while the 1972 year-class was comprised of 100% introduced fish. Small mesh samples of 1972 year-class fish, taken in 1974 and 1975 supported the earlier results (Table 2).

Since the 1971 year-class became vulnerable to the standard gill net gang in 1973, MDH isozyme samples were taken to determine relative contributions of introduced fish to the catch. A total of 51, 202, and 152 walleye of various year-classes were examined for MDH phenotypes during 1973-1975 (Table 3). In 1973 the 1971 year-class contained 50% introduced fish.

Figure 2. Age-frequency distributions of the catch from 1972-1975 indicating the contribution of introduced fish to the native population .



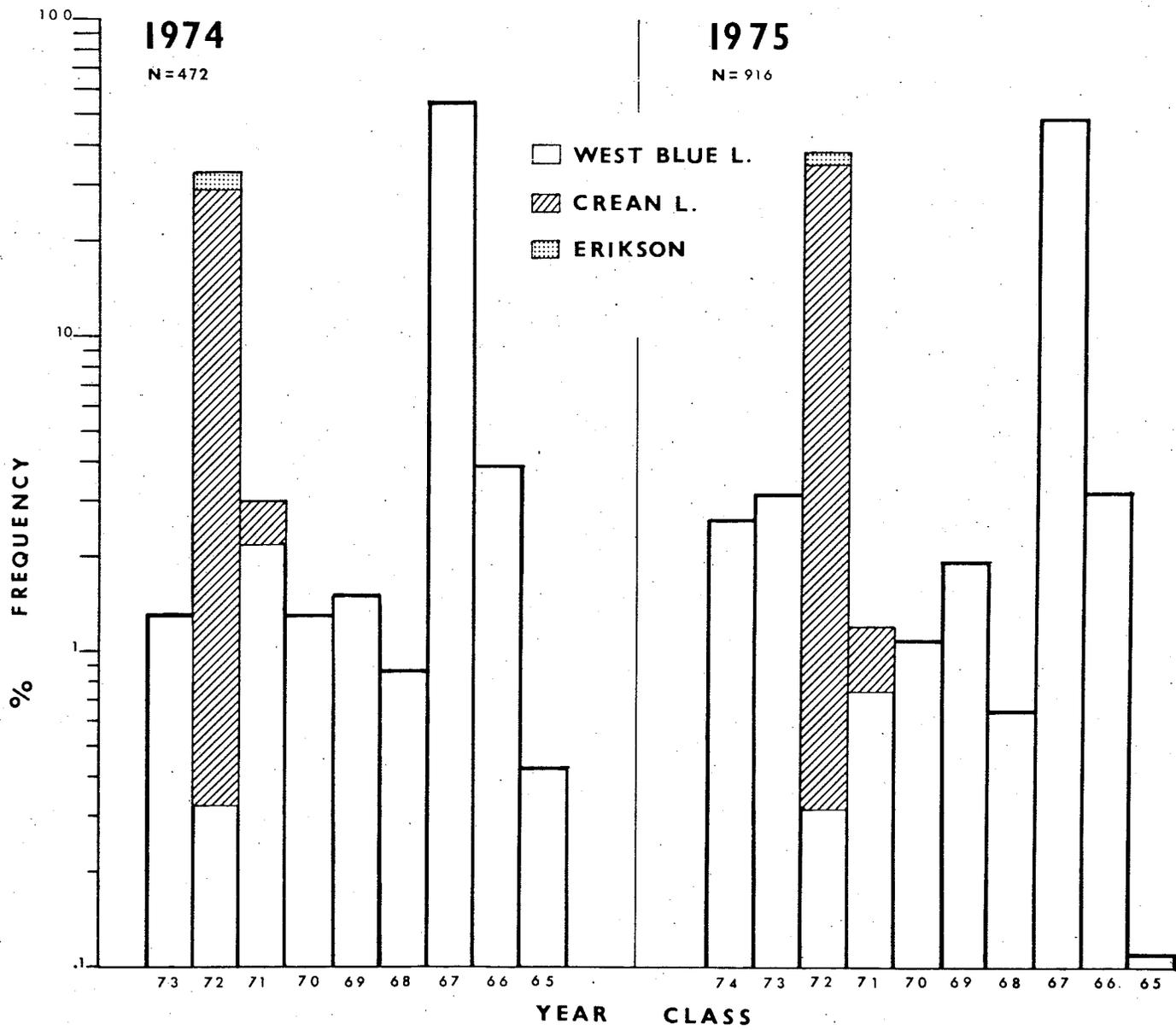


Table 2. Frequency of MDH isozyme phenotypes from small mesh gillnet catches, 1972-1975, for 1971 and 1972 introductions.

Year	Phenotypes										Totals		Crean Lake Fraction	
	C_1C_1		C_1C_3		C_2C_2		C_2C_3		C_3C_3		1971	1972	1971	1972
	1971	1972	1971	1972	1971	1972	1971	1972	1971	1972				
1972	8	-	2	-	5	-	4	-	0	-	19	-	.526	-
1973	0	19	0	17	0	0	0	0	0	0	0	36	-	1.00
1974	0	6	0	4	0	0	0	0	0	0	0	10	-	1.00
1975	0	2	0	0	0	0	0	0	0	0	0	2	-	1.00
Grand Totals											19	48		

Table 3. Frequency of MDH isozyme phenotypes in walleye from standard gillnet gang catches 1973-1975.

Year Class	Phenotypes															Totals			Crean Lake Fraction				
	C ₁ C ₁			C ₁ C ₃			C ₂ C ₃			C ₂ C ₂			C ₃ C ₃			73	74	75	73	74	75		
	73	74	75	73	74	75	73	74	75	73	74	75	73	74	75								
1973	0	0	0	-	0	0	-	0	1	-	3	4	-	0	2	0	3	7					
1972	0	50	60	-	45	54	0	2	1	0	0	1	0	0	0	0	97	116	0	.979	.983		
1971	1	1	2	2	2	1	3	4	2	0	3	2	0	1	1	6	11	8	.50	.27	.375		
1970	0	0	0	0	0	0	5	2	1	3	2	0	2	1	0	10	5	1					
1969	0	0	0	0	0	0	2	1	1	1	1	0	0	1	0	3	3	1					
1968	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	2	0					
1967	0	0	0	0	0	1	13	31	14	13	37	13	4	10	0	30	78	18					
1966	0	0	0	0	0	0	1	0	1	0	3	0	1	0	0	2	3	1					
															Totals			51	202	152			

By 1974 both augmented year-classes were fully vulnerable to the standard gang and were comprised of 27 and 97.9% introduced fish. A similar proportion was found in 1975 when the 1971 year-class comprised 37.5% and the 1972 year-class 98.3% introduced fish. Assuming the proportions of introduced fish in MDH samples from small mesh and standard gang samples (Tables 2, 3) are representative of those in the population the combined results of all MDH samples suggest the 1971 year-class to be 43% and the 1972 year-class 98.5% introduced fish.

The abundant 1967 and 1972 year-classes contributed over 80% to the total catch in all four years (Table 1). The other year-classes were uniformly less than 5% of the total catch (Fig. 2). The 1971 year-class is very weak, about average, even considering the 43% augmentation by introduced fish. In contrast, the abundant 1972 year-class constituted 33.1% of annual catch in 1974 and 37.9% in 1975. Again the whole year-class (98.5%) is introduced with only 4 native fish, 2 each in 1974 and 1975, being found in MDH samples (Table 3).

The fingerling introduction from Erikson also did not augment the population to any significant degree comprising 8.97% of the catch of 1972 year-class fish in 1974 and 6.92% in 1975. The single 1972 year-class fish captured in 1973 was of Erikson origin.

In 1975 the fish in the augmented year-classes were at a size desirable for a sport fishery and introduced fish, 3 and 4 year olds, constituted 35.7% of the adult population thus making quite a significant potential contribution to the harvestable stock.

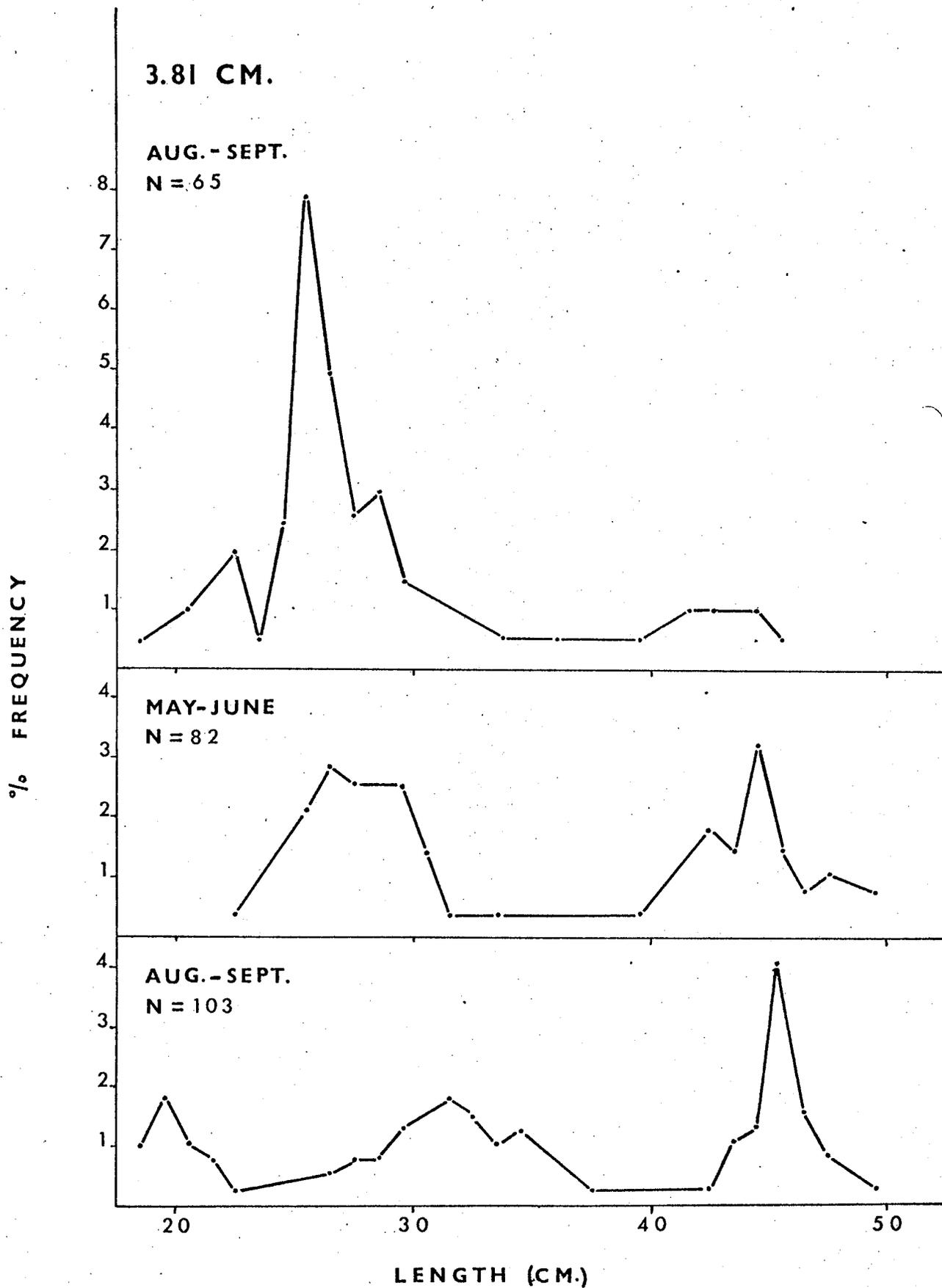
III Abundance

(i) Assumptions of Mark and Recapture Experiments

The models of all mark and recapture experiments require the validity of a number of assumptions whose violation can produce inaccuracies in the estimates of the parameters of interest. Possibly the most important assumption and the one least likely to be fulfilled is that of random sampling. The effects of selection by the sampling gear on the population will directly affect the length-frequency and age-frequency distributions so obtained (Fig. 2).

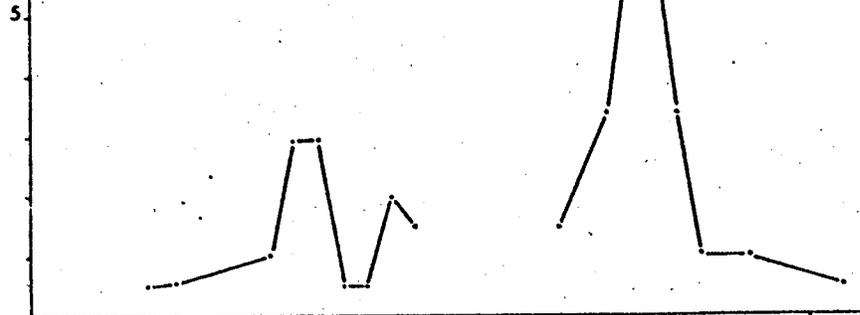
Length frequency curves (Fig. 3) of the catch from each mesh size in the standard gill net gang at six sampling times indicate that a wide range of lengths are sampled. The similarity of the curves at the three times particularly at the greater lengths, 400-500 mm, where the fish are slow growing and the target population stable indicates a relatively constant

Figure 3. Length-frequency curves for the three meshes in the standard gillnet gangs for 1974-1975.

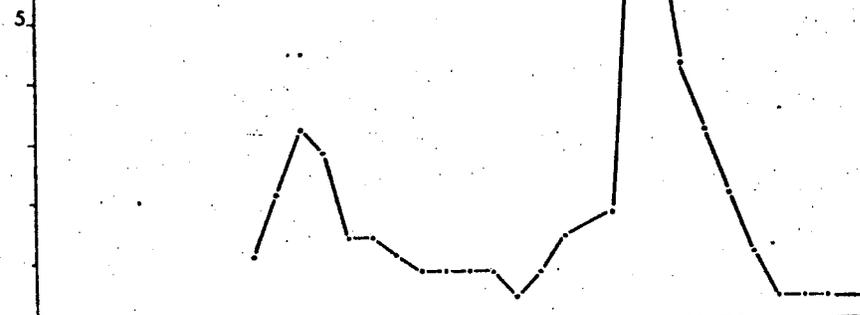


6.35 CM.

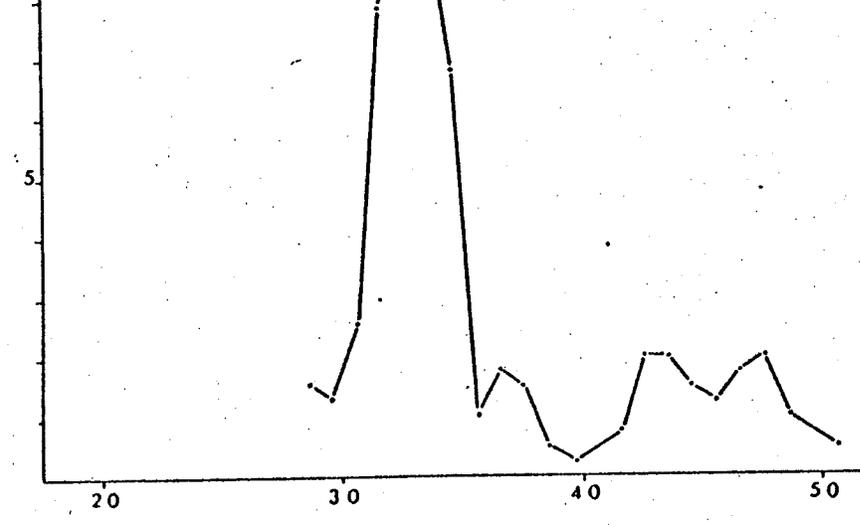
AUG. - SEPT.
N = 74



MAY - JUNE
N = 130



AUG. - SEPT.
N = 228

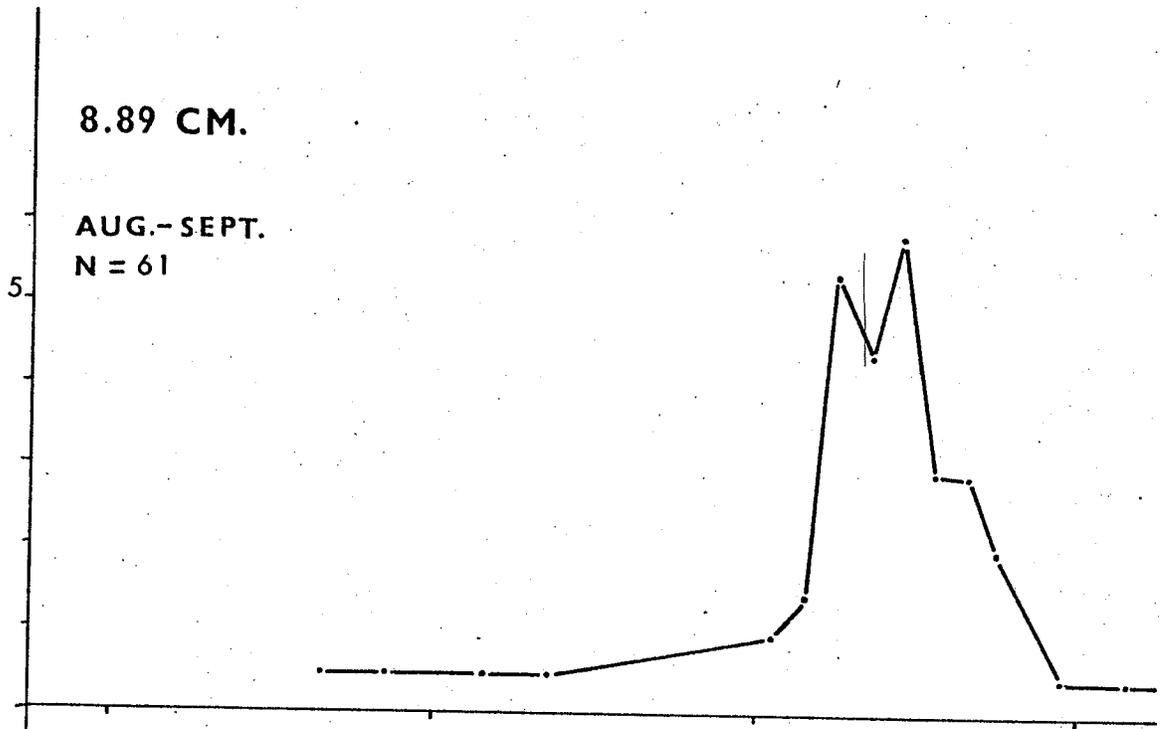


% FREQUENCY

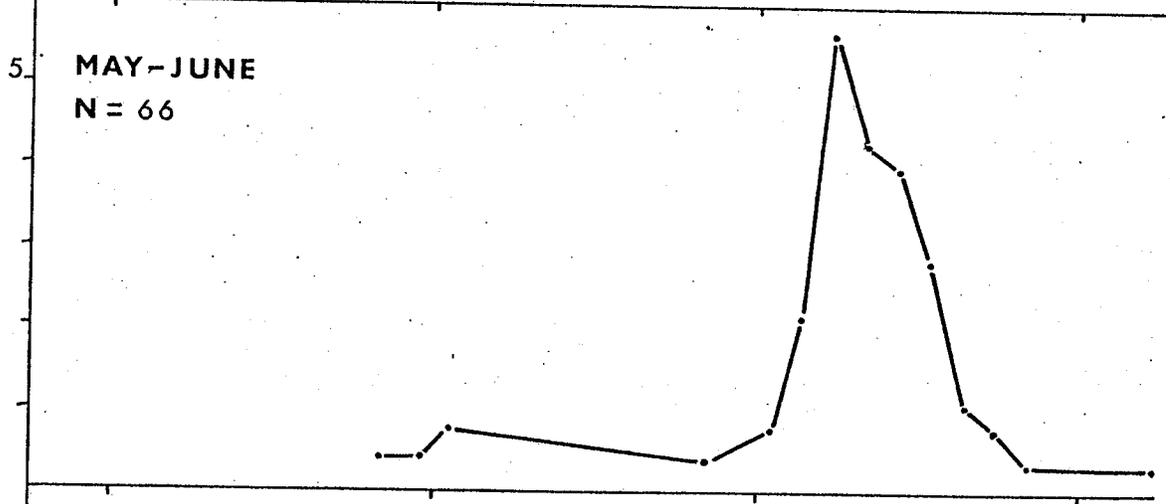
LENGTH (CM)

8.89 CM.

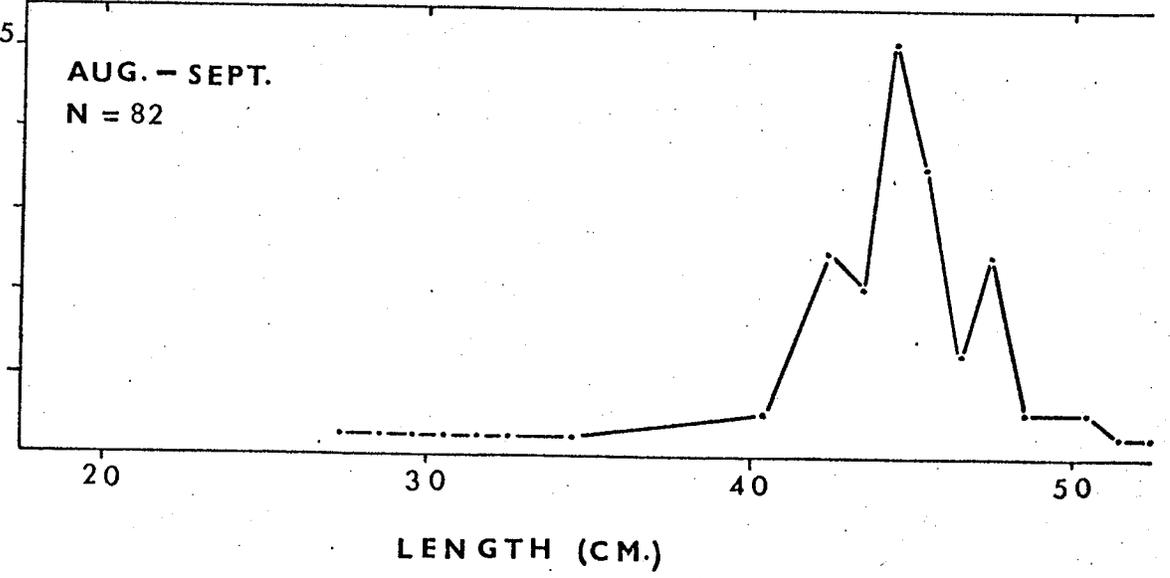
AUG.-SEPT.
N = 61



MAY-JUNE
N = 66



AUG. - SEPT.
N = 82



range of selection and efficiency of the sampling gear. The large peaks in the 3.81 cm mesh in the fall of 1974 at 250 mm and in the 6.35 cm mesh at 330 mm in the fall of 1975 probably reflects the fast growth of the 1972 year-class fish. The missing peak for this group in the spring of 1975 reflects the disproportionate number of larger active spawning fish in the catch rather than gear selection.

Generally, the total proportions of individuals of a given length sampled in a standard gang is very similar, save that the peaks at smaller sizes shift to the right with time as a result of growth (Fig. 3). This suggests that samples are probably negligibly biased by actual gear selection.

The absence of gear selection is supported also by the catch-per-unit of effort index which is fairly stable both within and between years (Table 4). If active selection for a particular length class were occurring for each mesh size then the rapid growth of the relatively larger number of small fish should produce marked fluctuations in this index of relative abundance. Since this appears not to be the case selection is inferred to be insignificant and samples random with respect to net selection.

Table 4. Catch-per-unit effort (No. of fish/standard gang/day) for the standard gang samples seasonally and annually.

Date	Catch	Effort (No. of gangs)	No. of Days fished	Catch/ unit effort	Mean
					catch/ unit effort
1972					
May 17-31	143	6	6	3.97	
June 24-July 7	79	6	6	2.19	
July 18-26	32	4	3	2.67	
Sept. 13-19	130	7	7	2.65	2.87
1973					
May 16-28	114	10	5	2.28	
June 12-19	98	6	3	5.44	
July 9-Aug. 8	130	10	7	1.86	
Aug. 20-25	117	12	6	1.63	
Sept. 10-17	110	10	5	2.20	2.68
1974					
May 21-June 1	121	14	7	1.24	
June 17-20	162	10	5	3.24	
Aug. 13-18	106	9	5	2.34	
Sept. 14-17	97	8	4	3.03	2.48
1975					
May 15-20	235	17	5	2.76	
June 15-19	271	17	5	3.19	
Aug. 5-11	235	22	6	1.78	
Sept. 2-6	214	14	4	3.82	2.89

The second major assumption in mark and recapture experiments is that mortality occurs equally among marked and unmarked individuals. Handling mortality was examined during 1974 by holding members of both groups in large tanks on the lakeshore with the following results:

Date	Size (mm)	Control		Tagged & Biopsied	
		Released	Died	Released	Died
June 3-11	282-473	3	0	6	0
June 17-24	161-234	3	1	3	3
Aug. 16-20	254-437	4	0	4	0

Appreciable mortality occurred only among the smaller fish in late June when water temperatures exceeded 20°C. Since all the experimental and one member of the control group expired this situation may not realistically reflect natural conditions. The application of Robsons (1969) 2 x 2 contingency table tests for "type I" or handling mortality failed to demonstrate any significant mortality with all calculable chi-squares being non-significant at the .05 probability level (Table 5). Therefore mortality attendant to marking is probably an inconsequential source of bias.

The third major assumption is that of equal catchability of marked and unmarked members of the population. In the majority of mark and recapture

Table 5. Chi-square contingency table tests to detect initial tagging mortality.

Date	No. captured at time i and released		No. recaptured at time i and released		Chi-square (Yates correction)	Significance level ($\alpha = .05$)
	No. seen later	No. not seen again	No. seen later	No. not seen again		
1972						
June 30	6	61	0	0	-	-
July 22	0	20	0	3	-	-
Sept. 16	16	114	0	1	1.3410	ns ^a
1973						
May 20	20	82	0	7	.6270	ns
June 16	5	81	1	4	.0997	ns
July 14	1	101	1	7	.9492	ns
Aug. 16	5	103	1	9	.0002	ns
Sept. 14	0	107	0	3	-	-
1974						
May 26	8	93	1	5	.0001	ns
June 19	7	115	0	10	.0018	ns
Aug. 16	13	86	0	3	.0427	ns
Sept. 15	25	72	1	4	.0563	ns
1975						
May 18	44	191	6	26	.0566	ns
June 17	24	207	4	45	.0440	ns
Aug. 8	6	192	4	34	2.7607	ns

^a non-significant

samples (Table 6) less than 20% of all individuals ever recaptured from a given marking period are recaptured in the first recapture period following the initial marking suggesting that a proportion of the recently marked population may not be available for recapture until a few months after marking. Equal catchability is also affected by the randomness of sampling and appears to be the most serious source of bias in this study.

The last major assumption is that the mark does not become detached. Tag loss will severely bias estimates of population abundance determined by either the Jolly-Seber (1965) or Chapman (1952) models although the latter may be corrected for this violation. Application of Gullands' (1963) model yields a loss rate of 31% per month, $r^2 = .313$, based on double tagging during 1975. The model of Robson and Regier (1966) is more comprehensive but requires a permanent mark. Since no individuals lost both marks during 1975 it was deemed applicable to the double-tagging data. Tag retention was estimated as 93% with all tests of the model non-significant (Appendix 1).

During routine sampling in 1974 fish bearing tag stubs (Table 6), i.e., the nylon "T" was embedded in the flesh but the numbered streamer had become detached,

Table 6. Number of walleye from standard gang samples captured, marked, released and recaptured in West Blue Lake from 1972-1975.

	No. of fish			Recaptures from Marking Periods																
	Captured	Released	Stubs ^a	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1972																				
1 May 17-31	143	114	-	-																
2 June 24-July 7	79	72	0	-	-															
3 July 18-26	32	20	0	2	1	-														
4 Sept.13-19	121	121	1	0	1	0	-													
	<u>375</u>	<u>327</u>																		
1973																				
5 May 16-23	114	102	0	0	2	0	5	-												
6 June 12-19	98	86	1	0	1	0	2	1	-											
7 July 9-19	116	103	5	0	0	0	5	2	1	-										
8 Aug.20-25	131	109	3	0	0	0	1	3	1	1	-									
9 Sept.10-17	110	108	1	1	0	0	0	2	0	0	0	-								
	<u>569</u>	<u>514</u>																		
1974																				
10 May 21-31	121	102	2	0	0	0	0	2	1	0	1	0	-							
11 June 17-21	162	87	4	1	1	0	1	3	0	0	1	0	3	-						
12 Aug.13-18	106	100	3	1	0	0	1	0	0	0	0	0	0	1	-					
13 Sept.14-17	97	97	3	0	0	0	0	2	0	0	0	0	0	0	2	-				
	<u>486</u>	<u>386</u>																		
1975																				
14 May 15-20	235	235	11	0	0	0	0	3	2	0	2	0	3	2	3	11	-			
15 June 15-19	270	231	12	1	0	0	0	3	0	0	1	0	1	3	3	13	25	-		
16 Aug.5-11	228	191	3	0	0	0	0	1	0	0	1	0	0	0	4	3	14	17	-	
17 Sept.2-6	214	214	8	0	0	0	0	0	0	0	0	0	1	1	4	2	13	8	10	-
Totals	947	871	57	6	6	0	18	22	5	1	6	0	9	7	16	29	52	25	10	

^a Represents recaptured nylon tag stubs from marks applied May 31, 1972 to Sept. 17, 1973.

began to appear in the samples quite regularly. This apparently resulted from glue failure (Mr. Amick, President, Floy Mfg. Co., personal communication) but did not affect tags applied during 1974 and 1975. This introduced irreconcilable bias into estimates for 1972 and 1973 (Appendix 2). On the whole correction for tag loss did not significantly improve the abundance estimates indicating either that the tag loss model is not appropriate or that tag loss is not a serious source of bias in the models for population estimation in this study.

(ii) Population Dynamics

Estimates of population size (\hat{N}_i), survival ($\hat{\phi}_i$) and recruitment ($\hat{\beta}_i$) for 1974 and 1975 sampling periods were determined by the Jolly-Seber birth and death model (Table 7). As previously mentioned estimates of population size based on the Chapman (1952) approach corrected for tag loss (Appendix 2) still produced biased estimates for 1972 and 1973 based on the criteria of Robson and Regier (1964) suggesting that the formulated tag loss model for 1975 did not adequately describe the tag disengagement phenomenon for 1972 and 1973. Consequently only the Jolly-Seber estimates for 1974 and 1975 warranted further consideration.

Table 7. Estimates of population size (\hat{N}_i), mortality ($\hat{\phi}_i$), recruitment ($\hat{\beta}_i$), and their standard errors from the birth and death model of Jolly (1965).

Date ^a	n_i	m_i	S_i	R_i	Z_i	α_i	M_i	N_i	$\hat{\phi}_i$	$\hat{\beta}_i$	$(\text{Var } \hat{N}_i)^{1/2}$	$(\text{Var } \hat{\phi}_i)^{1/2}$	$(\text{Var } \hat{\beta}_i)^{1/2}$
1974													
May 26	121	0	102	8	0	-	0	-	.7831	-	-	.4164	-
June 19	162	3	122	7	5	.0245	79.875	3255	.4001	2971	2320	.1735	3230
Aug. 16	106	1	99	13	11	.0187	79.571	4257	.4783	742	3331	.1449	2146
Sept.15	97	2	97	25	22	.0306	84.923	2774	.8401	-547	1687	.1832	1387
1975													
May 18	235	19	235	49	28	.0848	151.160	1784	.8770	473	482	.1915	454
June 17	271	42	231	28	35	.1581	322.0	2037	.9594	1051	493	.3347	615
Aug. 8	235	38	198	10	25	.1653	490.273	2967	-	-	1047	-	-
Sept.4	214	35	214	0	0	.1628	-	-	-	-	-	-	-

^a Refers to midpoint of sampling period.

Jolly-Seber estimates of abundance (\hat{N}) indicate a stable population of generally between 2000-3000 individuals (Table 7). Seasonally recruitment and mortality interact to modify the abundance. Survival ($\hat{\phi}$) exceeded 80% during all intervals except June-September 1974 when it dropped below 50% but this value appears to be biased by the high population estimates for June and August with large standard errors. These inflated population estimates appear to result partly from tag loss which didn't affect data collected during 1975.

The catch curve analysis of Robson and Chapman (1961) yields similar estimates of survival (Table 8) exceeding 80% in all four years. The lower estimates for 1974 and 1975 may reflect increased mortality of the 1967 year-class. The significant chi-squares are the result of the abnormally large recruitment of the 1972 year-class (Appendix 3).

Estimates of recruitment ($\hat{\beta}_i$) in 1974 tend to be inflated with large standard errors possibly the result of tag loss. Recruitment occurred primarily during the summer period, early June through late August.

The June-August 1974 recruitment of 2,971 is almost equal to the adult population and is composed primarily of 1972 year-class fish. Recruitment from August through September 1974 is 742, less than 15% of

Table 8. Annual mortality rates determined from the catch curve analysis of Robson and Chapman (1961) for 1972-1975.

Year	Estimate of Survival (S)	95% Confidence Interval	Heincke Estimate	Chi-Square (1 d.f.)	Probability of Greater Chi-Square
1972	.977	.968 < S < .986	.989	.381	~ .55
1973	.964	.959 < S < .969	.980	.953	~ .30
1974	.835	.824 < S < .846	.665	90.666	< .001
1975	.830	.822 < S < .838	.968	115.063	< .001

the adult population. The negative value in September results from overestimates of the population in June and August 1974 (Table 7).

Estimates of recruitment during 1975 are excellent with a magnitude of 1,524 over the May-August period. The majority again occurs from June-August. The impact of these young fish on the catch is also apparent in Table 1.

The magnitude of the large introduced 1972 year-class was estimated by the Jolly(1965) no birth model (Table 9) and indicated about 1500 individuals in the fall of 1974. The figure decreased sharply overwinter to about 800 individuals in the fall of 1975. Survival tends to be quite high during all sampling intervals for these fast growing juvenile members of the population.

IV Growth

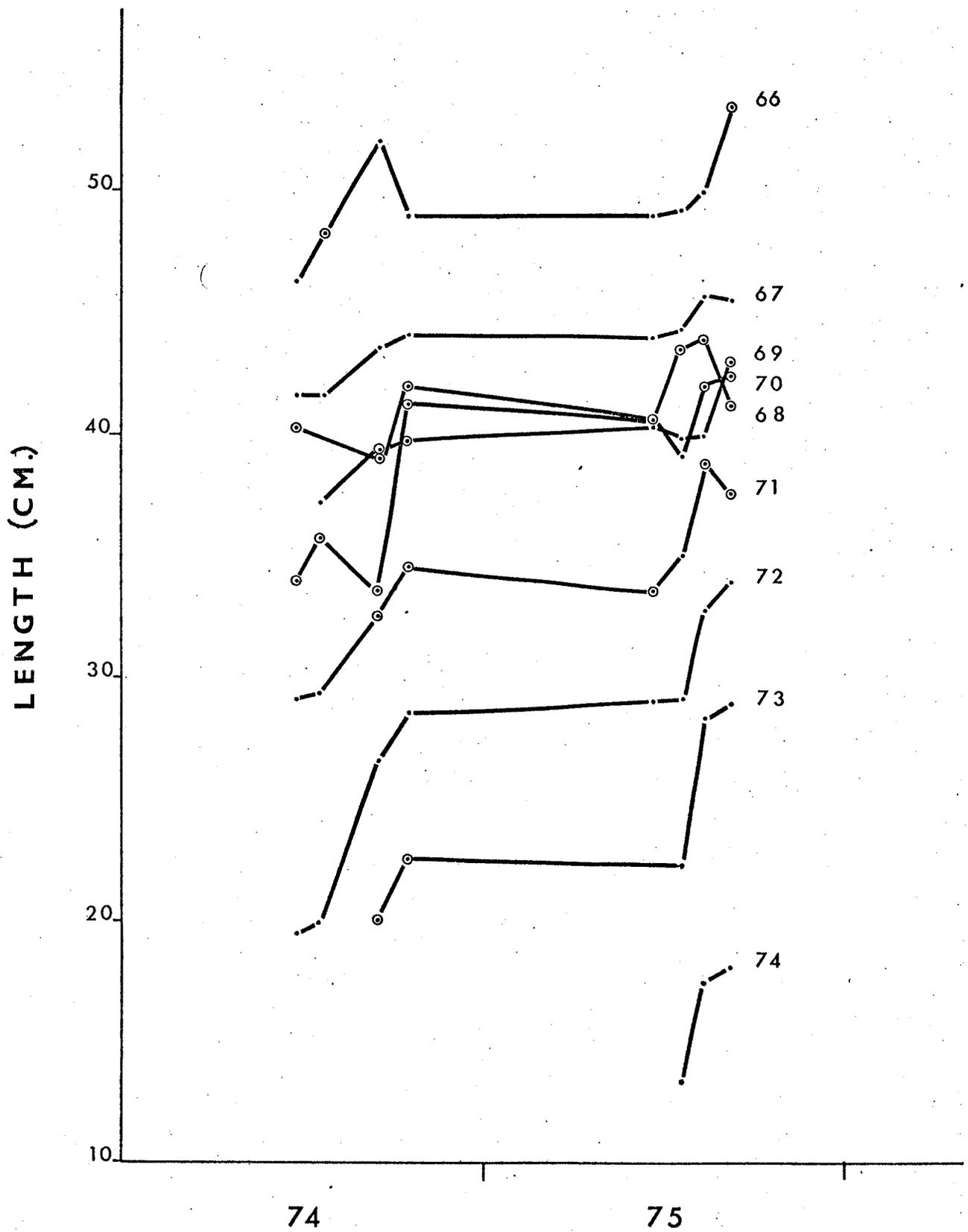
The samples from standard gill net catches provide the data to determine growth rates both directly from length measurements and indirectly through back-calculation from scales. Direct estimates of growth in length suffer from small sample size and non-random sampling (Fig. 4) which can produce marked variability in the observed growth curves.

Table 9. Estimates of population size (\hat{N}_i) and survival ($\hat{\phi}_i$) for the 1972 year-class based on the death but no birth model of Jolly (1965).

Date ^a	n_i	m_i	S_i	R_i	Z_i	Σn_{i0}	Z_i'	\hat{N}_i	$(\text{Var } \hat{N}_i)^{1/2}$	$\hat{\phi}_i$	$(\text{Var } \hat{\phi}_i)^{1/2}$
1974											
Aug. 16	37	0	35	6	1	311	312	1597	533	.909	.4303
Sept. 15	35	1	35	6	6	277	283	1450	484	.389	.1485
1975											
May 18	31	2	31	14	10	248	258	564	102	1.484	.3789
June 17	105	11	92	20	13	154	167	837	149	1.065	.3446
Aug. 8	99	21	99	10	12	146	88	891	239	-	-
Sept. 4	98	22	98	0	0	0	0	-	-	-	-

^a Refers to midpoint of sampling period

Figure 4. Growth in length (cm) of walleye year-classes during 1974-1975 (circles indicate three or fewer observations per mean, numbers refer to year-classes).



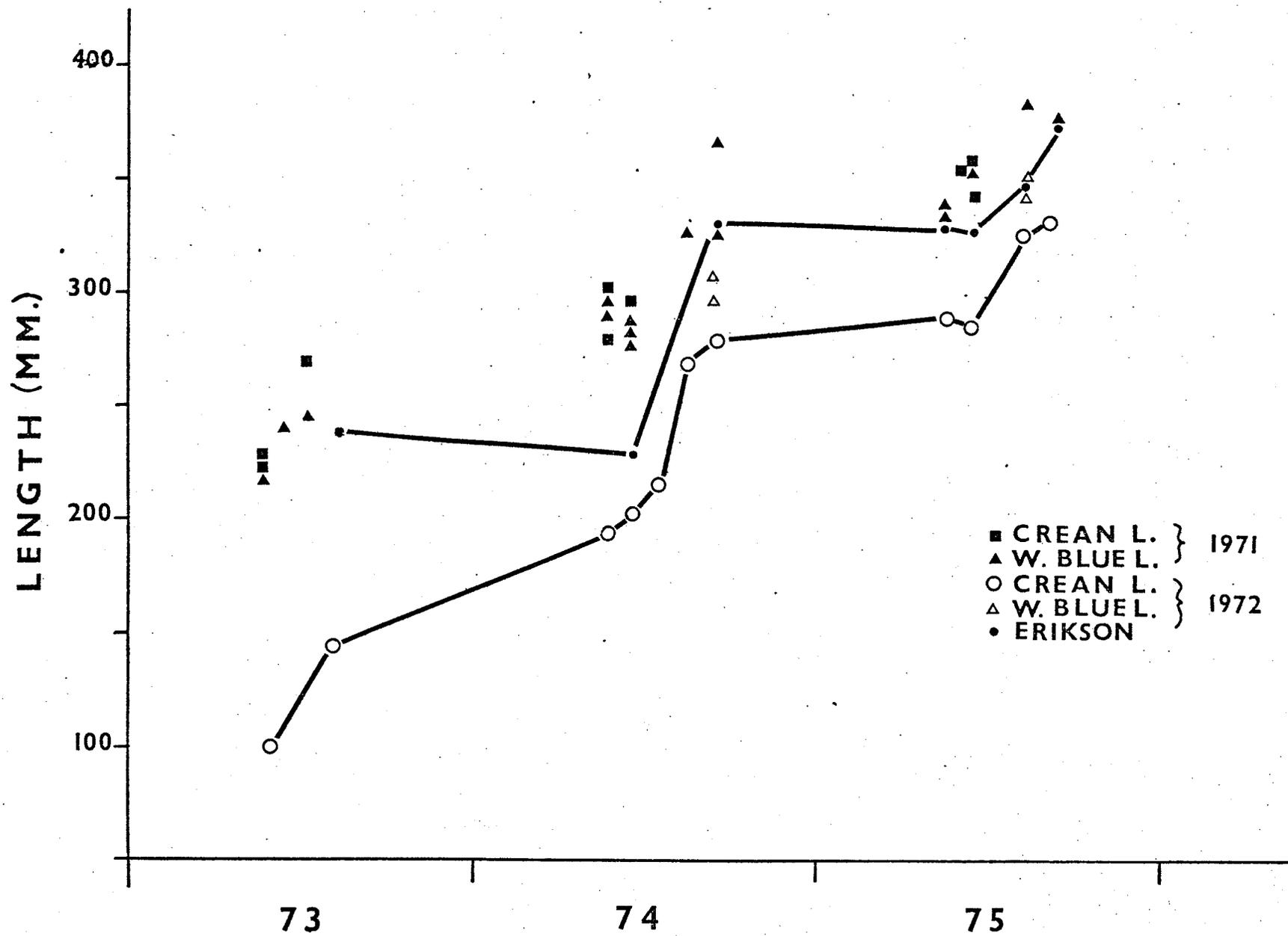
Seasonally, the growth rate changes markedly, being greatest in the June to August period for the 1971-1974 year-classes. The older fish also demonstrate marked growth during this interval. Growth in length is fastest in the 1 to 3 year olds of the order of 30 to 20% of the total length, respectively over the summer of 1975. Four to seven year olds indicate some growth but its magnitude is obscured by the variability resulting from small sample size. The few older individuals apparently experience negligible growth and some of the variability observed is probably the result of errors in ageing.

Growth of fish introduced in 1971 and 1972 relative to the native fish from these year-classes is of considerable interest in assessing the success of the plants. The native and introduced fish of both year-classes are similar in length at all times (Table 10). There is no noticeable difference in size of the native and introduced 1971 year-class fish and the four native fish of the 1972 year-class fall within the 95% confidence interval for introduced 1972 fish suggesting equivalence of growth of native and introduced fish throughout (Table 10). Relative growth of the 1971 and 1972 year-classes may be examined by comparing lengths of 1972 fish with those of 1971 fish the previous year. They are generally

Table 10. Length (mm) of walleye of known MDH phenotype captured from 1973 through 1975 with 95% confidence intervals where possible (Sample size in parenthesis).

Year	1973				1974					1975			
	May 20	June 13	July 9	Aug. 6	May 26	June 19	July 13	Aug. 15	Sept. 15	May 17	June 17	Aug. 8	Sept. 4
Native													
1971	220	240	245	-	289 294	282 + 15.5 (3)	-	325	326 365	335 336	352	382	376
1972	-	-	-	-	-	-	-	-	291 301	-	-	338 343	-
Introduced													
1971	222 222	-	258	-	279 300	296	-	-	-	-	349 + 26.7 (3)	-	-
1972	-	99 + 13.1 (13)	-	144 + 15.5 (13)	194 + 26.4 (14)	202 + 31.4 (45)	215 + 29.9 (8)	268 + 38.7 (18)	279 + 38.0 (18)	287 + 34.6 (22)	285 + 35.3 (31)	326 + 25.5 (30)	332 + 23.8 (29)
Erikson													
1972	-	-	-	238	-	228 + 56.0 (7)	-	332 336	326 + 24.9 (5)	314 341	324 + 57.1 (6)	345 + 46.7 (7)	376 + 33.7 (9)

Figure 5. Comparative growth in length (mm) of native and introduced members of the 1971 and 1972 year-classes during 1973-1975.



comparable although the 1971 year-class fish appear to have grown slightly faster (Fig. 5).

Erikson fish are significantly larger than the other 1972 year-class fish throughout (Table 10), reaching the same length as 1971 fish by August of 1974 (Fig. 5). This may be the direct result of enhanced growth and larger size when planted since there is no evidence of greater growth rate once planted in West Blue Lake. Erikson fish were also heavier at all times from 1973-1975 averaging 50% greater in weight than other 1972 year-class fish (Table 11).

Instantaneous rates of growth determined directly from lengths frequently demonstrate negative trends (Fig. 4) which although possible for individuals are unlikely to occur in whole year-classes. To compensate weighted linear regression equations were fitted to weights for all year-classes in 1974 and 1975 and instantaneous rates determined from predicted weights (Appendix 4). The resultant growth rates are similar to those determined directly but negative trends occur only during winter. The poor fit obtained for most year-classes suggests that a linear model does not adequately describe the growth based on so few individuals.

Seasonal growth was also determined indirectly from scales by back-calculation of lengths at previous annuli.

Table 11. Relative abundance and weight of Erikson and Crean Lake fish of the 1972 year-class from standard gang catches. (Standard deviation in parentheses).

Date	Crean Lake		Erikson		
	Frequency in Catch	\bar{w} (gm)	Frequency in Catch	\bar{w} (gm)	% Frequency
			1973		
Aug. 7	32 ^a	35.0 (24.95)	1	189.4	
Total	0		1		100.
			1974		
May 26	14	59.9 (12.1)	0	-	
June 19	63	64.9 (29.1)	7	101.8 (33.3)	
Aug. 16	35	155.2 (47.6)	2	330.8 (8.9)	
Sept. 16	30	189.0 (51.3)	5	307.6 (26.6)	
Total	142		14		8.97
			1975		
May 18	29	208.3 (48.9)	2	312.7 (57.4)	
June 17	97	214.1 (59.3)	6	305.5 (66.4)	
Aug. 8	119	311.4 (47.3)	7	368.3 (64.4)	
Sept. 4	79	337.7 (68.0)	9	482.9 (60.3)	
Total	323		24		6.92

^a captured in small mesh nets.

Results obtained from analysis of covariance precluded pooling all the data from 1972 to 1975, chi-square test for homogeneity of variance, $\chi^2_{3d.f.} = 52.857$, $P < .005$ (Appendix 5).

Individual regression equations for the total length-scale radius relationship are:

$$1972 \quad L = 6.3123 S \ .7880$$

$$1973 \quad L = 9.1926 S \ .7132$$

$$1974 \quad L = 7.9622 S \ .7535$$

$$1975 \quad L = 6.3662 S \ .7958$$

where L is total length in mm and S is scale radius x 46.5 in mm.

Back-calculated lengths at scale annuli are variable for different year-classes but fairly similar within year-classes (Appendix 6).

Seasonal instantaneous growth in length relative to the last annulus is expectedly very different for young and older individuals. Growth rate varied by almost one order of magnitude between 3⁺ and 8⁺ fish during 1975 (Appendix 7). No consistency existed between rates determined directly from lengths and those back-calculated from scales but since the former requires fewer assumptions it is probably the most realistic given reasonable sample sizes.

Since all estimates of weight are determined directly from the length-weight relation, trends in weight are analagous to those for lengths although more variable.

V Production

Seasonal changes in biomass are the result of recruitment, mortality, and growth. Their interaction results in the formation of new biomass or production.

The determination of production by the Chapman variant of the Ricker (1946) approach requires instantaneous growth rates and population estimates. The small size of many year-classes precluded individual population estimates. To circumvent this problem, year-class abundance was apportioned from the total population estimate on the basis of the percentage contribution to the catch at the particular sampling period. This produced fluctuations in the abundances determined for all year-classes over the year but the validity of this approach is demonstrated below.

Annual production for the period August 1974 to August 1975 was determined by the three separate methods of calculating growth rate (Table 12, Appendix 8, 9). Results were very comparable, the direct approach (Table 12) estimates annual production at 340.97 kg. The production

Table 12. Production and biomass estimates for the 1966-1973 walleye year-classes as determined by the arithmetic approach.

	Year Class	Mean Weight \bar{w} (g)	Abundance \bar{N}	Biomass B (kg)	Inst. daily Growth G	Mean Biomass \bar{B} (kg)	Production ^a P (kg)	Annual Production (kg)	$\frac{P}{B}$
June 19	1966	1077	63	67.85					
	1974	1967	674	1428	962.47				
		1968	-	-	-				
		1969	464	63	29.23				
		1970	411	63	25.89	.00404	173.53	40.71	.235
		1971	219	168	36.79	.00237	1335.40	183.43	.137
		1972	67	1470	98.49	-	-	-	-
				<u>1220.72</u>	.00295	37.21	6.40	.172	
					-.00341	19.86	-3.94 ^b	.000	
Aug. 16	1966	1362	205	279.21	.00560	24.61	7.98	.324	
	1974	1967	773	2210	1708.33	.01539	174.23	156.98	.901
		1968	544	41	22.30		1764.84	350.86	.199
		1969	551	82	45.18				
		1970	337	41	13.82				
		1971	303	41	12.42	-.00673	204.72	-41.33	.000
		1972	165	1515	249.98	.00125	1392.71	52.23	.038
		1973	65	123	8.00	.00762	30.59	7.08	.228
				<u>2308.96</u>	.00147	39.30	1.42	.036	
					.02201	16.36	10.81	.661	
Sept. 15	1966	1113	117	130.22	.00681	16.70	3.47	.208	
	1974	1967	802	1343	1077.09	.00746	227.27	50.86	.224
		1968	684	58	39.67	.01237	9.56	-	-
		1969	576	58	33.41		1935.61	84.54	.044
		1970	652	29	18.91				
		1971	372	58	21.58	.00005	73.78	.90	.012
		1972	206	993	204.59	-.00006	1058.10	-15.56	.000
		1973	95	117	11.12	.00045	22.29	-2.46	.000
				<u>1562.26</u>	.00026	36.01	2.29	.064	

TABLE 12 CONT'D ON NEXT PAGE

Table 12. Production and biomass estimates for the 1966-1973 walleye year-classes as determined by the arithmetic approach.

	Year Class	Mean Weight w (g)	Abundance N	Biomass B (kg)	Inst. daily Growth G	Mean Biomass \bar{B} (kg)	Production ^a P (kg)	Annual Production (kg)	P/B
May 18	1966	1126	126	141.88	-.0030	14.31	-1.04		.000
	1967	792	1312	1039.10	-.00044	12.12	-1.31		.000
	1968	613	8	4.90	.00017	128.62	5.36		.042
	1969	613	63	38.62	-	-	-		-
	1970	607	16	9.71	-	-	-		-
	1971	334	8	2.67	-	-	-		-
	1972	215	244	52.46	.00119	102.45	3.66		.036
	1973	-	-	-	.00103	932.55	28.82		.031
					<u>1128.20</u>				.218
June 17	1966	1167	54	63.02	-.00090	30.62	-1.74		.000
	1967	817	1011	825.99	-.00296	13.46	1.20		.089
	1968	762	15	11.43	.00068	113.28	2.30		.141
	1969	580	39	22.62	-	-	-		.020
	1970	555	31	17.21	-	-	-		-
	1971	384	46	17.66	-	-	-		-
	1972	219	795	174.11	.00036	62.42	1.17		.019
	1973	92	46	4.23	.00194	762.91	73.22		.096
					<u>1293.20</u>				.027
Aug. 8	1966	1189	52	61.83	.00021	18.93	.21		.011
	1967	903	775	699.83	.00411	17.55	3.75	-35.60	.213
	1968	783	26	20.36	.00627	19.23	5.27	138.70	.326
	1969	586	26	15.24	.00723	350.87	131.97	6.86	.376
	1970	688	26	17.89	.01483	17.84	13.76	2.18	.771
	1971	533	39	20.79	-	-	-	14.71	.182
	1972	319	1554	527.63	-	-	-	9.87	
	1973	199	158	31.44	-	-	-	190.49	
					<u>1240.04</u>		13.76		
					Aug. 1974-Aug. 1975 $\Sigma P = 340.97$				

^a Production is the product of instantaneous growth rate (G) and mean biomass (\bar{B}) and the number of days between the midpoints of adjacent sampling periods.

^b Estimates of negative production were taken as zero for determining P:B ratios.

based on predicted weights (Appendix 8) is 346.41 kg while that determined indirectly by back-calculation is 367.09 kg (Appendix 9). Estimates for the earlier June-August 1974 period uniformly exceeded the annual estimates apparently due to the inflated estimates of population size. The majority of annual production occurred during the June-August period (68%), 25% in the late summer (August-September), 4% was lost overwinter, and the remaining 11% accrued in the spring after ice-out. The majority of total annual production resulted from the two strong year-classes, 1972 (56%) and 1967 (41%). The total stock biomass was quite constant at 1200-1300 kg while the mean annual biomass (\bar{B}) was 1506.5 kg, an overestimate resulting from the high August 1974 estimate of abundance (Table 12).

The majority (71%) of this mean annual biomass results from the 1967 year-class (1070 kg) while only 16% (242 kg) is from 1972 fish. The rate of production is exemplified by the ratio of production to the mean biomass. Annually this figure is .237 for the whole population, while for the 1967 year-class it is .134, and .929 for the 1972 fish (Table 12). Seasonally the ratio approaches .20 in the summer, June to August period, but is virtually zero for the remainder of the year (Table 12). It is also apparent that the turnover rate for the smaller fish is much higher than for older slow growing individuals.

The graphical technique of Allen (1951) provides a convenient check of the Chapman production estimates. Graphs (Fig. 6) were constructed for the 1967 and 1972 year-classes based on estimates of the population from Table 12. The two approaches yield comparable estimates, 144.1 kg, as opposed to the 138.7 kg obtained arithmetically for 1967 fish. Similarly, the 1972 estimate of 181.5 kg graphically is consistent with the arithmetic estimate of 190.5 kg.

The production of introduced fish was also examined. The 1972 year-class was subdivided into Erikson and introduced fish and the respective Chapman estimates of 3.85 kg and 167.60 kg were obtained (Table 13). Similarly, for the 1971 year-class 4.24 kg or 43% of annual production was contributed by introduced fish. *In toto* introduced fish account for 175.69 kg or 51.5% of annual production for August 1974 to August 1975.

Of particular interest in regard to the accuracy of the production values is the validity of assessing abundance from frequency (Table 12) in the catch. Comparison of this approach to the results for the 1972 year-class estimates by mark and recapture using Jolly's (1965) no-birth model (Table 9) lends support to this argument. Estimates of abundance and production by both methods and estimates obtained by fitting curves to the abundances prior to formulating production are presented below:

Figure 6. Estimates of production for the 1967 and 1972 year-classes of walleye based on the graphical approach for 1974-1975 (Figures are annual production in kg, dots are abundances from proportion in catches, circles are predicted from curve fitted to abundances).

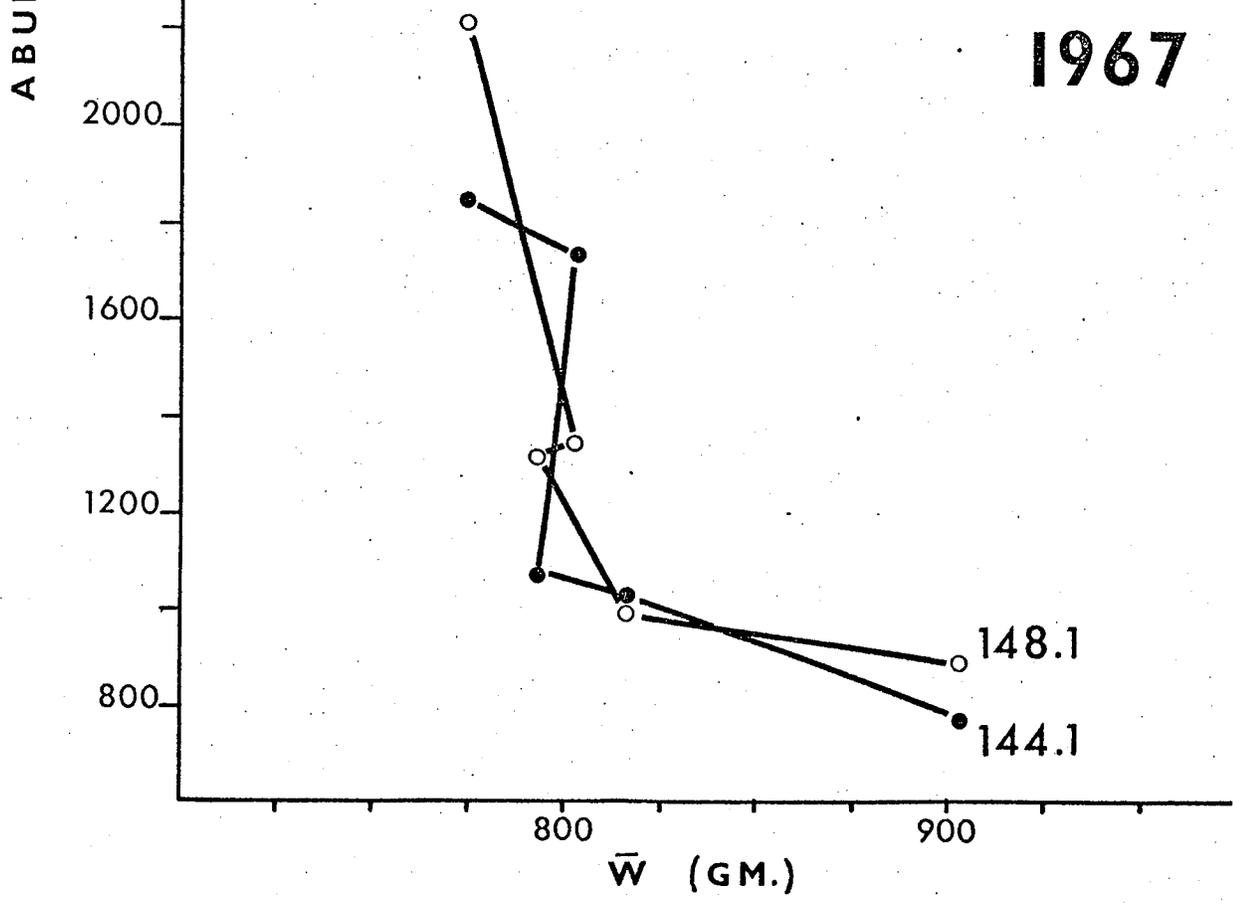
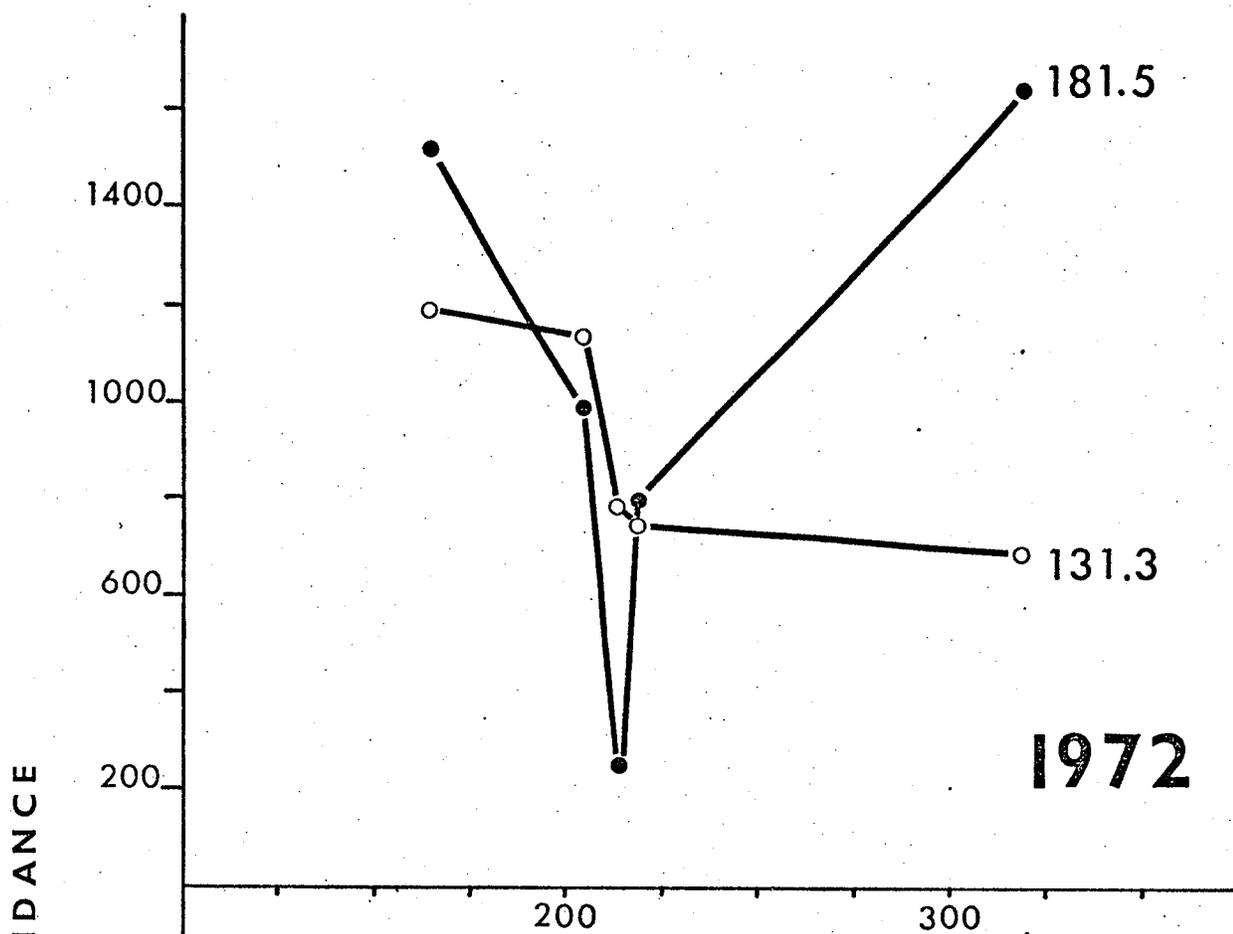


Table 13. Production estimates for fry (Crean L.) and fingerlings (Erikson) from the 1972 introduction based on the arithmetic procedure during 1974-1975.

Date ^a		Mean Weight \bar{w} (g)	Abundance N	Biomass (kg)	\bar{B} (kg)	Inst. Growth G	Production (kg)	Annual Production (kg)
Aug. 16	Crean L.	155	1377	213.4				
	Erikson	331	117	38.8	192.0	.198	38.10	
Sept. 15	Crean L.	189	902	170.6	31.3	-.072	-2.25	
	Erikson	308	77	23.7	108.4	.095	10.38	
May 18	Crean L.	208	222	46.1	14.8	.016	.24	
	Erikson	313	19	5.9	100.4	.028	2.86	
June 17	Crean L.	214	722	154.6	12.4	-.026	-.32	
	Erikson	305	62	18.8	311.0	.374	116.25	
Aug. 8	Crean L.	311	1503	467.5	32.9	.188	6.18	167.60
	Erikson	368	128	47.1				3.85

^a Refers to midpoint of the sampling period

Date	Jolly no birth	Predicted from curve	Jolly birth&death	Predicted from curve
Aug. 16	1597	1492	1515	1191
Sept. 15	1450	1398	993	1137
May 18	564	821	244	782
June 17	837	769	795	747
Aug. 8	891	687	1654	690
Production (kg)	165.7	141.6	181.5	131.3

The similarity of the production estimates by these two independent methods supports the method of apportioning abundance employed herein although there is a suggestion that slight overestimation occurred in the Chapman estimates (Table 12) because of bias in abundances in the catches possibly from net selection or behaviour differences seasonally.

The greater information content in the Chapman estimates overrides the effects of this slight bias and suggests that on the whole production estimates can inspire confidence as accurate and realistic reflections of walleye production dynamics in West Blue Lake.

DISCUSSION

An important determinant in the success or failure of fry plants is the viability of the fry at the time of the introduction. The severe egg and embryo losses and poor condition of the fry planted in 1971 resulting from transport and handling prevented accurate enumeration of healthy fry planted. In 1972 a small field hatchery on the lakeshore permitted careful monitoring of fry development and an exact census of numbers released into West Blue Lake (Ward and Clayton 1975).

Samples of yearlings in 1972 and 1973 (Table 2) indicated that significant numbers of introduced fry had survived and made important contributions to their respective year-classes (Ward and Clayton 1975). The isozyme analysis of samples taken in the standard gillnet gangs from 1973-1975 (Table 3) confirmed the earlier findings and indicated that the introductions had made a significant contribution to the native walleye population (Fig. 2).

Natural year-class strength varies significantly (Fig. 2) and the smaller 1971 introduction composed almost half of this rather weak year-class. Conversely, the larger 1972 introduction produced a virtually complete artificial year-class rivalling the dominant native 1967 year-class in abundance. In addition, the constancy of the proportions of introduced fish in the year-classes (Table 3) over the

three years suggests that no differential mortality of native and introduced individuals occurred.

The ultimate criterion of the success or failure of fish stocking must rest on its ability to contribute significantly to the production of the adult or harvestable portion of the population.

The accuracy of estimates of production will depend largely on those of population size (Chapman 1967). The importance of failure of assumptions in mark and recapture experiments in terms of biasing population estimates is examined extensively in theory (Cormack 1968 Seber 1973; Ricker 1975) but seldom in practice.

Attempts have been made wherever possible to evaluate the extent and nature of the biases in the estimates of population parameters since some biases are inevitable and if not serious probably compensatory.

The importance of gillnet selection as a source of non-random or unrepresentative samples was recently reviewed by Hamley (1975). At best, the situation is unresolved because of the multitude of variables involved whose individual importance is difficult if not impossible to quantify. Hamley and Regier (1973) determined selectivity curves for walleye by fishing a known marked population and determined that the selectivity curves are bimodal and increase in amplitude with mesh size. Kelso and Ward (1972)

determined that although differential efficiency of mesh sizes probably occurred all sizes of fish were represented in the catch. The present data (Fig. 3) support this finding and suggest that only the small fast growing individuals may be significantly affected by gillnet selection. However, since proportions of fishes taken in the 3.89 cm mesh and subsequently in the 6.35 cm mesh are similar the efficiency of the two meshes is probably not sufficiently different to warrant concern about the randomness of the samples. Temporally changes occur in the frequency of catch by mesh size but these changes result from growth rather than selection and no evidence of differential efficiency by mesh is apparent so samples realistically reflect the size composition of the population.

Equal mortality of marked and unmarked individuals was examined by holding members of both groups in tanks on the lakeshore. The death of one control fish in June 1974 suggests that conditions were probably unrepresentative of those occurring *in situ*. McDonald (1969) has found approximately 10% tagging mortality in walleye from holding experiments in pens in a lake. However, the chi-square contingency table tests of Robson (1969) indicated no significant difference between the proportions of fish captured once and those captured several times (Table 5) suggesting that negligible mortality resulted from the handling and marking process.

The assumption of equal catchability of marked and unmarked fish may be tested given sufficient data (Seber 1973). Unfortunately the paucity of recapture data precludes rigorous statistical testing of this assumption. The observed temporal distribution of recaptures (Table 6) suggests that fish may temporarily become immobile and unavailable for immediate recapture. Carothers (1973) applied computer simulation to the unequal catchability problem and suggests it to be "an unattainable ideal." Ryder (1968) found that walleye tagged at the same time tended to be recaptured together suggesting that individual schools of walleye may contain unrepresentative numbers of tagged individuals. Therefore fish within schools are probably not randomly distributed and by implication the populations of marked and unmarked fish will not be equally catchable. This probably represents one of the most serious sources of bias in the present mark and recapture experiments.

The retention of marks is the most obviously violable assumption directly reducing the number of marked individuals available for recapture and produces overestimates of population size. Although a statistically acceptable agreement was obtained with the model proposed by Robson and Regier (1966) estimating less than 10% tag loss per month, the proportion of fish recaptured who had lost anchor tags approached 50% during periods of high water temperature and fast growth (Appendix 1). Rawstrom (1973) also reports a loss rate of about 10% but found the anchor

tags to be as good or better than others tested in terms of retention and ease of application. Tag loss was definitely insignificant during 1975 but may have contributed slightly to overestimation in 1974 estimates of abundance.

Present estimates of abundance are quite precise relative to other literature with very large confidence intervals (Chapman 1967) although slight overestimation appears to occur in June and August 1974 (Table 7) apparently the result of unequal catchability and possibly tag loss. In general no gross violation of the assumptions for mark and recapture experiments are apparent so observed estimates of population parameters accurately reflect population dynamics.

Abundance (Table 7) is similar to that reported previously by Kelso and Ward (1972) although the distribution of year-class strengths during 1969 was more uniform at a time when the strong 1967 year-class was just entering the catchable stock. Seasonal changes are also similar with mortality largely restricted to the overwinter and spring post-spawning periods. The populations were both subject to continuous recruitment by 1+ and 2+ individuals during the summer. Mortality is much less than the 60-80% reported Kelso and Ward (1972), usually only 10-20% (Table 7) between most sampling periods from mark and recapture data, and 3-17% annually from the catch curve analysis (Table 8). These values are comparable to the estimates for lightly exploited walleye populations reported by Forney (1966) 5%,

Olson (1958) 5%, and Mraz (1968) 10%. They are much less than those reported by Ricker (1949) and Healey (1975a) for lightly exploited whitefish populations.

Recruitment was estimated at 3713 for 1974 and 1524 for 1975 (Table 7) the former a gross overestimate but still of a magnitude similar to that reported by Kelso and Ward (1972).

The accuracy of population parameters is supported by Kelso and Ward (1972) but must be complemented by accurate growth determinations to result in representative production figures. Theoretical curves are available for describing average annual population growth (Paloheimo and Dickie 1965) but seasonal growth has been infrequently examined. Exceptions are Gerking's (1966a, b) studies of sunfish and the earlier walleye studies at West Blue Lake (Glenn 1969, Kelso and Ward 1972). These studies and the present one found that most of the annual growth occurred from June to late August (Fig. 4). Gross population growth (Appendix 6) is comparable to that of most temperate walleye populations (Scott and Crossman 1973).

Instantaneous growth rates were determined by several methods (Table 12, Appendix 4, 7) and produced essentially comparable results. Growth rates determined directly from lengths (Table 12) require only that samples be representative of the population. Present results are not directly comparable to the other walleye studies since growth was determined over

different time intervals and all three studies were plagued by small sample sizes for some year-classes resulting in variabilities in the growth rates and some anomalous negative values.

To overcome irregular past growth history and unrepresentative samples growth rates are often back-calculated from scales (Glenn 1969). This approach is applicable to seasonal growth (Appendix 7) as well (Gerking 1966a, b, Glenn 1969, Kelso and Ward 1972) but requires the establishment of a relationship between scale radius and total length. Many workers have used linear regression equations (Forney 1965, Mraz 1968, Glenn 1969, Kelso and Ward 1972) which appear to overestimate lengths at early annuli. Others have applied polynomials of various orders (Carlander 1945, Moenig 1975, Smith and Pycha 1961) fitted algebraically or by eye (Eschmeyer 1950). Hile (1970) emphasizes that a polynomial is applicable to any data set. The method employed in this study is that of Monastrysky (Tesch 1968) used previously by Hile (1941) for his rock bass study. The biological relevance of this form of relationship is fully documented by Gould (1966). Again all three walleye studies suffer from small sample sizes but growth rates are of the same magnitude (Table 12, Appendix 4, 7). Since the direct approach requires only random sampling it is favoured as the basis for production calculations.

No comparable literature exists on the growth of introduced fry (Fig. 5) but mean weights (Table 11) are similar to those reported for native fish by Kelso and Ward (1972) suggesting similar growth rates. Fingerlings transferred from the ponds at Erikson, Manitoba were considerably larger than those in the lake apparently the result of warmer temperatures and abundant food, possibly cannibalism (Scott, *et al.*, 1951). The relatively large size of pond reared walleye has been noted by Lawler, *et al.* (1974) and is comparable to that reported by Churchill (1963) for Nebish Lake where fall stocking from rearing ponds also occurred.

The age composition of the population is considerably different from that expected for unexploited northern populations (Johnson 1972, 1973) with over 80% of the annual 1975 catch being composed of the 1967 and 1972 year-classes rather than by a preponderance of older individuals. In 1975, 38% of the catch resulted from 1972 (3+) year-class fish (Table 1). Glenn (1969) also found that the 1963 (3+) and 1964 (4+) year-classes predominated in 1966-1967 while Kelso and Ward (1972) found the 1967 (2+) and 1964 (5+) year-classes to be abundant in 1969-1970 suggesting that no stable age distribution exists and weaker year-classes are the rule with the occasional abundant year-class to revitalize the population. It is also apparent that although the strong 1972 year-class is artificial no depressing effect of the introduction is evident since both the 1973 and 1974 natural

year-classes are abundant and support the thesis of natural fluctuations in abundance (Fig. 2) of unexploited populations. This is entirely consistent with the observed fluctuations in abundance of many exploited populations (Carlander 1945, Hile 1954, Smith and Krefting 1954, Regier, *et al.* 1969) and will of course effect fluctuations in production of the population as a whole from year to year.

Production in fish populations has most frequently employed the instantaneous approach (Gerking 1962, Mann 1965, Ricker and Foerster 1948) or the arithmetic variant (Chapman 1968, Healey 1975b, Kelso and Ward 1972). Recent emphasis has centered on the graphical approach (Allen 1951, LeCren 1962, Moenig 1975, O'Conner and Power 1976, and Crisp, *et al.* 1974), but all methods should yield similar estimates. The present study determined annual production in 1974-1975 as 340.97 kg ($.42 \text{ gm/m}^2$) using the arithmetic approach. (Table 12). Kelso and Ward (1972) determined production as 340.31 kg ($.42 \text{ gm/m}^2$) using growth rates back-calculated from scales. This approach yields 366.72 kg ($.45 \text{ gm/m}^2$) in the present work (Appendix 8). The graphical approach was applied to the 1967 and 1972 year-classes which comprised 87% of the 1975 biomass (Table 12) and supported results from the arithmetic method. Comparable figures for production are scarce but walleye production is low relative to salmonid populations (Chapman 1967). Production is similar to the

.14 - .51 gm/m²/yr reported for pike in Windermere by Johnson (1966) and that for other walleye populations, Moenig (1975) .127 - .256 gm/m²/yr for Dexter Lake in northwestern Ontario, and Hofmann (1972) .339 - .756 gm/m²/yr for Oneida Lake. Production figures should be incremented 5-10% for gonadal production. Mann (1965) reports gonad production for four species in the Thames River at about 10% and Allen (1951) found egg production in brown trout approximated 10%. Crisp, *et al.* (1974) found eggs contributed 5-10% to total production in trout and less than 5% in bullhead.

The percid studies all concentrated on the older members of the population although a number of workers have found that the majority (60-80%) of production occurs in the youngest members (1-3 yr olds) of the population (Allen 1951, Horton 1961, Gerking 1962, Mathews 1971, O'Conner and Power 1975). Production studies on introduced fish are non-existent but during 1974-1975 introduced fish were 3+ and 4+ years old and contributed the majority (51.5%) of the total annual population production a result consistent with findings for native populations and indicates that fish introductions may indeed significantly augment natural population production. The production by introduced fish resulted almost entirely (95%) from the 1972 fry plant with the remainder split evenly between the 1971 fry plant and the fingerlings from Erikson each contributing about 1% of annual population production.

At best fingerling plants appear to have the same potential as poor fry plants in terms of augmenting population production.

Success of fry plants appears to be partially correlated to stocking density. Early studies (Hile 1937, Carlander 1945, Smith and Krefting 1954) employing low stocking densities (.004 - .030 fry/m²) showed minimal effects on year-class strength while higher densities (.45 - 2.35 fry/m²) indicated apparent enhancement of year-classes (Rose 1955, Forney 1975, 1976, Carlander, *et al.* 1960). Similarly the 1971 fry plant at West Blue Lake (.06 - .12 fry/m²) met with limited success while the .457 fry/m² planted in 1972 produced excellent results.

In contrast, fingerling plants have nowhere vindicated themselves. Olson and Wesloh (1962) and Johnson (unpublished data) were unable to detect increases in gillnet catches from unmarked fingerling plants. Schneider (1969) reports less than 5% returns of marked fingerlings while Kempinger and Churchill (1972) and Jennings (1970) found returns of 13 and 10% to creel censuses in successful stockings, others were uniformly low of the order of 1 to 2%. The fingerling plant in West Blue Lake in 1972 (Table 11) also met with marginal success, only 7 to 9% returns in gillnet catches from 1973-1975.

Explanations for the apparent superiority of fry as opposed to fingerling plants, are not readily apparent. It is almost axiomatic that recruitment is a function of stock biomass (Ricker 1954, 1975; Beverton 1962, Beverton and Holt 1957) although Bagenal (1973) demonstrated that fecundity

varies to regulate population abundance with small populations producing more eggs/unit stock than the converse. Inevitably the initially large egg production experiences overwhelming mortality within a short time of spawning and year-class strength appears to be fixed by the end of the first year. Advocates of density-independent environmental regulation as a causal mechanism are numerous. Doan (1942) found temperature and turbidity to be major factors in walleye and sauger year-class success. Similarly, temperature has frequently been cited as foremost in regulating egg and fry survival (Christie 1963, Lawler 1965, Christie and Regier 1973, Svardson and Molin 1973). Recently Busch, *et al.* (1975) demonstrated that walleye year-class strength varied with rate of water warming and frequency of storms. No such relationships were apparent for West Blue Lake. Salmonid populations apparently experience severe density-dependent mortality (LeCren 1962, 1965, 1973; Backiel and LeCren 1967). Ward and Larkin (1964) and Johnson (1965) emphasized the importance of compensatory mortality through predation although the latter also emphasizes space and consequently food limitation in year-class success.

Forney (1976) proposes a similar mechanism for walleye suggesting that year-class strength is determined directly by compensatory mortality through cannibalism. It appears that large year-classes of perch dampen this predation (Forney 1974) at the same time enhancing young walleye growth (Forney 1966)

since perch are the primary food source of young walleye in many lakes. Chevalier (1973) also demonstrated that walleye tend to cannibalize smaller members of the fry population so rapid growth should enhance first year survival. The result is a simple predator-prey situation controlling perch year-class strength (Forney 1971) with high walleye survival increasing predation on perch and the reduced perch population inducing increased cannibalism on the walleye fry (Forney 1974).

Forney (1976) suggests that stocking fry may increase the number of recruits but a strong year-class will suppress subsequent year-classes through cannibalism. The 1972 fry plant in West Blue Lake apparently didn't depress the 1973 and 1974 year-classes (Fig. 2) indicating the probable presence of a time lag in this effect. Supplemental planting will be valuable primarily in established populations where natural reproduction and survival are poor or where the rate of exploitation of the adults is high and predation on young of the year has reduced effects on survival (Forney 1976). It would appear that the walleye population in West Blue Lake is limited primarily by poor natural reproduction and that augmentation can produce significant results if yellow perch or an alternate food source are abundant. One may also conjecture that the differential success of the two fry plants aside from density differences relates to their chronology

relative to the hatching of their primary food, the yellow perch, since Forney (1966) emphasizes that the relative size of predator and prey determines the utility of the prey as a food source. The poor success of fingerling plants is inexplicable since their relatively larger size should yield a definite survival advantage although their inability to adapt to a new environment and food source may leave them excessively vulnerable to predation.

Although the present study quantifies the effects of fry and fingerling plants on year-class strength and production of the native population, it remains necessary to achieve a more complete understanding of population- and production-dynamics (Mann 1969) relative to the food supply before effective management strategies may be formulated. Paloheimo and Dickie (1970) and Dickie (1972) emphasize the importance of the production to biomass ratio in understanding the transfer efficiencies of predator and prey populations and consequently as an important component in the determination of potential yield to a fishery. The turnover rate of walleye in West Blue Lake in 1974 and 1975 is .237 comparable to the .34 determined by Kelso and Ward (1972) in 1969-1970. The difference appears to result from the greater proportion of population production by older fish in 1974-1975 than was the case in 1969-1970. Other literature values for walleye are similar, Moenig (1975) found .25 - .52 in Dexter Lake and Hofmann (1972)

.16 - .37 in Oneida Lake. Windberg, *et al.* (1972) report a value of .4 for predatory fish (pike, sander, and perch) in three Russian reservoirs. This suggests that West Blue Lake walleye production is representative of temperate *Stizostedion* sp. production, although lake morphometrics are uncharacteristic for walleye (Regier, *et al.* 1969) or sander (Deedler and Willemsen 1964), and provides a basis for future comparisons.

The application of electrophoresis to identify MDH phenotypes of native and planted fry has proved to be invaluable in assessing the introductions. Introduced fry are readily distinguishable from native fish throughout their lives allowing long term monitoring of their contribution to the native population. The MDH isozyme phenotypes are virtually 100% accurate. It appears that introductions of newly hatched walleye fry can significantly supplement natural production under appropriate conditions and if the survey by Clayton, *et al.* (1974) accurately reflects the restricted nature of the C¹ allele, walleye plants based on the isozyme phenotype marking system warrant consideration for future stocking studies in western Canada.

LITERATURE CITED

- Allen, K. R. 1951. The Horokiwi Stream: a study of a trout population. N. Z. Mar. Dep. Fish. Res. Div. Bull. Ner. Ser. 10:231 p.
- Backiel, T., and E. D. LeCren. 1967. Some density relationships for fish population parameters, p. 261-293. In S. D. Gerking (ed.). The biological basis of freshwater fish production. John Wiley and Sons, Inc. New York.
- Bagenal, T. B. 1973. Fish fecundity and its relations with stock and recruitment. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 164:186-198.
- Bell, R. K., and F. J. Ward. 1970. Incorporation of organic carbon by *Daphnia pulex*. Limnol. Oceanogr. 15:713-726.
- Beverton, R. J. H. 1962. Long-term dynamics of certain North Sea fish populations, p. 242-259. In E. D. LeCren and M. W. Holdgate (ed.). The exploitation of natural animal populations. Blackwell Scientific Publications, Oxford.
- Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II. Mar. Fish. G. B. Minist. Agric. Fish. Food. 19:533 pp.
- Busch, W.-D. N., R. L. Scholl, and W. L. Hartman. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960-70. J. Fish. Res. Board Can. 32:1733-1743.

- Carlander, K. D. 1945. Age, growth, sexual maturity and population fluctuations of the yellow pike-perch, *Stizostedion vitreum vitreum* (Mitchill) with reference to the commercial fisheries, Lake of the Woods, Minnesota. Trans. Am. Fish. Soc. 73:90-107.
- Carlander, K. D., Whitney, R. R. Speaker, E. B., and K. Madden. 1960. Evaluation of walleye fry stocking in Clear Lake, Iowa, by alternate-year planting. Trans. Am. Fish. Soc. 89:249-254.
- Carothers, A. D. 1973. Capture-recapture methods applied to a population with known parameters. J. Anim. Ecol. 42:125-146.
- Chapman, D. G. 1952. Inverse, multiple, and sequential sample censuses. Biometrics 8:286-306.
- Chapman, D. W. 1967. Production in fish populations. p. 3-29. In S. D. Gerking (ed.). The biological basis of freshwater fish production. John Wiley and Sons, Inc. New York.
- Chapman, D. W. 1968. Production, p. 182-196 In W. E. Ricker (ed.). Methods for assessment of fish production in fresh waters. IBP Handbook 3. Blackwell Scientific Publications, Oxford and Edinburgh.
- Chevalier, J. R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. Trans. Am. Fish. Soc. 102:739-744.

- Christie, W. J. 1963. Effects of artificial propagation and the weather on recruitment in the Lake Ontario whitefish fishery. J. Fish. Res. Board Can. 20:597-646.
- Christie, W. J., and H. A. Regier. 1973. Temperature as a major factor influencing reproductive success of fish - two examples. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer. 164:208-218.
- Churchill, W. S. 1963. The effects of fin removal on survival, growth, and vulnerability to capture of stocked walleye fingerlings. Trans. Am. Fish. Soc. 92:298-300.
- Clayton, J. W., and J. H. Gee. 1969. Lactate dehydrogenase isozymes in longnose and blacknose dace (*Rhinichthys cataractae* and *R. atratulus*) and their hybrid. J. Fish. Res. Board Can. 26:3049-3053.
- Clayton, J. W., D. N. Tretiak, and A. H. Kooyman. 1971. Genetics of multiple malate dehydrogenase isozymes in skeletal muscle of walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 28:1005-1008.
- Clayton, J. W., R. E. K. Harris, and D. N. Tretiak. 1974. Geographic distribution of alleles for supernatant malate dehydrogenase in walleye (*Stizostedion vitreum vitreum*) populations from western Canada. J. Fish. Res. Board Can. 31:342-345.

- Cormack, R. M. 1968. The statistics of capture - recapture methods. *Oceanogr. Mar. Biol. Annu. Rev.* 6:455-506.
- Crisp, D. T., R. H. K. Mann, and J. C. McCormack. 1974. The populations of fish at Cow Green, Upper Teesdale, before impoundment. *J. Appl. Ecol.* 11:969-996.
- Cucin, D., and H. A. Regier. 1965. On the dynamics and exploitation of lake whitefish in southern Georgian Bay. *J. Fish. Res. Board Can.* 23:221-274.
- Deelder, C. L., and J. Willemsen. 1964. Synopsis of biological data on pike-perch *Lucioperca lucioperca* (Linnaeus) 1758. *FAO Fish. Synops.* 28:52 p.
- Dell, M. B. 1968. A new fish tag and rapid cartridge fed applicator. *Trans. Am. Fish. Soc.* 97:57-59.
- Dickie, L. M. 1972. Food chains and fish production. *Int. Comm. Northwest Atl. Fish. Spec. Publ.* 8: 201-219.
- Doan, K. H. 1942. Some meteorological and limnological conditions as factors in the abundance of certain fishes in Lake Erie. *Ecol. Monogr.* 12:293-314.
- Dymond, J. R. 1957. Artificial propagation in the management of Great Lakes fisheries. *Trans. Am. Fish. Soc.* 86:384-392.
- Eschmeyer, P. H. 1950. The life history of the walleye *Stizostedion vitreum vitreum* (Mitchill) in Michigan. *Mich. Inst. Fish. Res. Bull.* 3. 99 p.
- Forney, J. L. 1965. Factors affecting growth and maturity in a walleye population. *N.Y. Fish Game J.* 12: 217-232.

- Forney, J. L. 1966. Factors affecting first-year growth of walleyes in Oneida Lake, New York. N.Y. Fish Game J. 13:146-167.
- Forney, J. L. 1967. Estimates of biomass and mortality rates in a walleye population. N.Y. Fish Game J. 14:176-192.
- Forney, J. L. 1971. Development of dominant year classes in a yellow perch population. Trans. Am. Fish. Soc. 100:739-749.
- Forney, J. L. 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. Trans. Am. Fish. Soc. 103:15-24.
- Forney, J. L. 1975. Contribution of stocked fry to walleye fry populations in New York lakes. Prog. Fish. Cult. 37:20-24.
- Forney, J. L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) populations of Oneida Lake, New York, 1966-73. J. Fish. Res. Board Can. 33:783-792.
- Gerking, S. D. 1962. Production and food utilization in a population of bluegill sunfish. Ecol. Monogr. 32:31-78.
- Gerking, S. D. 1966a. Annual growth cycle, growth potential, and growth compensation in the bluegill sunfish in northern Indiana lakes. J. Fish. Res. Board Can. 23:1923-1956.

- Gerking, S. D. 1966b. Length of the growing seasons of the bluegill sunfish in northern Indiana. *Int. Ver. theor. angew. Limnol. Verh.* 16:1056-1064.
- Glenn, C. L. 1969. Seasonal rates of growth within a population of walleye, *Stizostedion vitreum vitreum* (Mitchill) in West Blue Lake, Manitoba during 1966-1967. M.Sc. Thesis. University of Manitoba, Winnipeg, Man. 63 p.
- Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biol. Rev. (Camb.)*. 41:587-640.
- Gulland, J. A. 1963. On the analysis of double-tagging experiments. *Int. Comm. Northwest Atl. Fish. Spec. Publ.* 4:228-229.
- Hamley, J. M. 1975. Review of gillnet selectivity. *J. Fish. Res. Board Can.* 32:1943-1969.
- Hamley, J. M., and H. A. Regier. 1973. Direct estimates of gillnet selectivity to walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Board Can.* 30:817-830.
- Healey, M. C. 1975a. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. *J. Fish. Res. Board Can.* 32:427-448.
- Healey, M. C. 1975b. Production in unexploited lake whitefish populations in northern Canadian lakes. *Int. Ver. theor. angew. Limnol. Verh.* 19:2371-2377.

- Hile, R. 1937. The increase in the abundance of the yellow pike-perch, *Stizostedion vitreum vitreum* (Mitchill), in Lakes Huron and Michigan, in relation to the artificial propagation of the species. Trans. Am. Fish. Soc. 66:143-159.
- Hile, R. 1941. Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque) in Nebish Lake, Wisconsin, Trans. Wis. Acad. Sci. Arts. Lett. 33:189-337.
- Hile, R. 1954. Fluctuations in growth and year-class strength of the walleye in Saginaw Bay. U. S. Fish Wildl. Serv., Fish. Bull. 56:7-59.
- Hile, R. 1970. Body-scale relation and calculation of growth in fishes. Trans. Am. Fish. Soc. 99:468-474.
- Hofmann, P. 1972. Consumption of young yellow perch (*Perca flavescens*) by a walleye (*Stizostedion vitreum*) population in Oneida Lake. Ph.D. Thesis, Cornell University, Ithaca, New York, 67 p.
- Horton, P. A. 1961. The bionomics of brown trout in a Dartmoor stream. J. Anim. Ecol. 30:311-338.
- Jennings, T. 1970. Progress report of Spirit Lake walleye studies status of marked fingerling stocking study. Iowa State Conserv. Comm. Quart. Biol. Rep. 22:49-56.
- Johnson, L. 1966. Consumption of food by the resident population of pike, *Esox lucius*, in Lake Windermere. J. Fish. Res. Board Can. 23:1523-1535.

- Johnson, L. 1972. Keller Lake: characteristics of a culturally unstressed salmonid community. J. Fish, Res. Board Can. 29:731-740.
- Johnson, L. 1973. Stock and recruitment in some unexploited Arctic lakes. Rapp. P.-V. Reun. Perm. Int. Explor. Mer 164:219-227.
- Johnson, W. E. 1965. On mechanisms of self-regulation of population abundance in *Oncorhynchus nerka*. Mitt. int. Verein. theor. angew. Limnol. 13:66-87.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration: a stochastic model. Biometrika 52:225-247.
- Kelso, J. R. M., and F. J. Ward. 1972. Vital statistics, biomass, and seasonal production of an unexploited walleye (*Stizostedion vitreum vitreum*) population in West Blue Lake, Manitoba. J. Fish. Res. Board Can. 29:1043-1052.
- Kempinger, J. J., and W. S. Churchill. 1972. Contribution of native and stocked walleye fingerlings to the angler's catch, Escanaba Lake, Wisconsin. Trans. Am. Fish. Soc. 101:644-649.
- Lawler, G. H. 1965. Fluctuations in the success of year-classes of whitefish populations with special reference to Lake Erie. J. Fish. Res. Board Can. 22:1197-1227.

- Lawler, G. H., L. A. Sunde, and J. Whitaker. 1974. Trout production in prairie ponds. *J. Fish. Res. Board Can.* 31:929-936.
- LeCren, E. D. 1962. The efficiency of reproduction and recruitment in freshwater fish, p. 283-296. In E. D. LeCren and M. W. Holdgate (eds.). *The exploitation of natural animal populations.* Blackwell Scientific Publications, Oxford.
- LeCren, E. D. 1965. Some factors regulating the size of populations of freshwater fish. *Mitt. Int. Verein. theor. angew. Limnol.* 13:88-106.
- LeCren, E. D. 1973. The population dynamics of young trout (*Salmo trutta*) in relation to density and territorial behaviour. *Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer* 164:241-246.
- Loftus, K. H., and H. A. Regier. (ed.). 1972. *Proc. Symp. on Salmonid Communities in Oligotrophic Lakes (SCOL).* *J. Fish. Res. Board Can.* 29:613-986.
- Mann, K. H. 1965. Energy transformations by a population of fish in the River Thames. *J. Anim. Ecol.* 34:253-275.
- Mann, K. H. 1969. The dynamics of aquatic ecosystems, p. 1-81. In J. B. Cragg (ed.). Vol. 6, *Advances in ecological research.* Academic Press, London.
- Mathews, C. P. 1971. Contribution of young fish to total production of fish in the River Thames near Reading. *J. Fish. Biol.* 3:157-180.

- McDonald, D. G. 1969. Post tagging mortality of pike, perch, walleye & rainbow trout following dart tag application. Alberta Fish Wildl. Div. Fish. Sect. Manag. Rep. 7:11 p.
- Moenig, J. T. 1975. Dynamics of an experimentally exploited walleye population in Dexter Lake, Ontario. M.Sc. Thesis, University of Toronto, Toronto, Ontario, 198 p.
- Mraz, D. 1968. Recruitment, growth, exploitation and management of walleyes in a southeastern Wisconsin lake. Wis. Dept. Natur. Resources Tech. Bull. 40: 38 p.
- O'Conner, J. F., and G. Power. 1976. Production by brook trout (*Salvelinus fontinalis*) in four streams in the Matamek watershed, Quebec. J. Fish. Res. Board Can. 33:6-18.
- Olson, D. E. 1958. Statistics of a walleye sport fishery in a Minnesota lake. Trans. Am. Fish. Soc. 87:57-72.
- Olson, D. E., and M. Wesloh. 1962. A record of six years of angling on Many Point Lake, Becker County, Minnesota with special reference to the effect of walleye fingerling stocking. Minn. Dep. Conserv. Invest. Rep. 247:7 p.
- Paloheimo, J. E., and L. M. Dickie. 1965. Food and growth of fishes. I. A growth curve derived from experimental data. J. Fish. Res. Board Can. 22:521-542.

- Paloheimo, J. E., and L. M. Dickie. 1970. Production and food supply, p. 499-527. In J. H. Steele (ed.), Marine Food Chains. Oliver and Boyd, Edinburgh.
- Parrish, B. B. (ed.). 1973. Proc. Symp. on Fish Stocks and Recruitment. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 164:372 p.
- Rawstrom, R. R. 1973. Comparisons of disk dangler, trailer, and internal anchor tags on three species of salmonids. Calif. Fish Game 59:266-280.
- Regier, H. A., V. C. Applegate, and R. A. Ryder. 1969. The ecology and management of the walleye in western Lake Erie. Great Lakes Fish. Comm. Tech. Rep. 15:101 p.
- Ricker, W. E. 1946. Production and utilization of fish populations. Ecol. Monogr. 16:373-391.
- Ricker, W. E. 1949. Mortality rates in some little-exploited populations of fresh-water fishes. Trans. Am. Fish. Soc. 77:114-122.
- Ricker, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559-623.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: xviii + 382 p.
- Ricker, W. E., and R. E. Foerster. 1948. Computation of fish production. Bull. Bingham Oceanogr. Collect. Yale Univ. 11:173-211.

- Robson, D. S. 1969. Mark-recapture methods of population estimation, p. 120-141. In N. L. Johnson and H. Smith (ed.). New Developments in Survey Sampling. John Wiley and Sons, Ltd., New York.
- Robson, D. S., and D. G. Chapman. 1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181-189.
- Robson, D. S., and H. A. Regier. 1964. Sample size in Petersen mark-recapture experiments. Trans. Am. Fish. Soc. 93:215-226.
- Robson, D. S., and H. A. Regier. 1966. Estimates of tag loss rates from recoveries of fish tagged and permanently marked. Trans. Am. Fish. Soc. 95:56-59.
- Roedel, P. M. (ed.). 1975. Proc. Symp. on Optimum sustainable yield as a concept in fisheries management. Am. Fish. Soc. Spec. Publ. 9:iii + 89 p.
- Rose, E. T. 1955. The fluctuation in abundance of walleyes in Spirit Lake, Iowa. Proc. Iowa Acad. Sci. 62:567-575.
- Ryder, R. A. 1968. Dynamics and exploitation of mature walleyes, *Stizostedion vitreum vitreum*, in the Nipigon Bay region of Lake Superior. J. Fish. Res. Board Can. 25:1347-1376.
- Schneider, J. C. 1969. Results of experimental stocking of walleye fingerlings, 1951-1963. Mich. Dep. Natur. Resources, Inst. Fish. Res. Rept. 1753:31 p.

- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: xi + 965 p.
- Scott, W. B., D. N. Omand, and G. H. Lawler. 1951. Experimental rearing of yellow pikeperch fry in natural waters. Can. Fish. Cult. 10:1-6.
- Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52:249-259.
- Seber, G. A. F. 1973. The estimation of animal abundance and related parameters. C. Griffen & Co., Ltd., London. xii + 506 p.
- Smith, L. L., Jr., and L. W. Krefting. 1954. Fluctuations in production and abundance of commercial species in the Red Lakes, Minnesota, with special reference to changes in the walleye population. Trans. Am. Fish. Soc. 83:131-160.
- Smith, L. L., Jr., and R. L. Pycha. 1961. Factors related to commercial production of walleye in Red Lakes, Minnesota. Trans. Am. Fish. Soc. 90:190-217.
- Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., New York. 481 p.
- Svardson, G., and G. Molin. 1973. The impact of climate on Scandinavian populations of the sander, *Stizostedion lucioperca* (L.). Inst. Freshwater Res. Drottningholm Rep. 53:112-139.

- Tesch, F. W. 1968, Age and Growth, p. 93-120. In
W. E. Ricker (ed.). Methods for assessment of fish
production in fresh waters. Blackwell Scientific
Publications, Oxford and Edinburgh.
- Uthe, J. F. 1971. A simple field technique for
obtaining small samples of muscle from living fish.
J. Fish. Res. Board Can. 28:1203-1204.
- Ward, F. J., and J. W. Clayton. 1975, Initial effects of
fry introduction on year-class strengths of West Blue
Lake walley, *Stizostedion vitreum vitreum* (Mitchill),
using fry with distinctive malate dehydrogenase
isozyme phenotypes as an identifying mark.
Int. Ver. theor. angew. Limnol. Verh. 19:2394-2400.
- Ward, F. J., and P. A. Larkin. 1964. Cyclic dominance in
Adams River sockeye salmon. Int. Pacific Salmon Fish.
Comm., Prog. Rept. 11:116 p.
- Ward, F. J., and G. G. C. Robinson. 1974. A review of
research on the limnology of West Blue Lake,
Manitoba. J. Fish. Res. Board Can. 31:977-1005.
- Winberg, G. G., V. A. Bobitsky, S. I. Gavrilov, G. V.
Gladky, I. S. Zakharenkov, R. Z. Kovaleoskaya, T. M.
Mikjeeva, P. S. Nevyadomskaya, A. P. Ostapenya, P. G.
Petrovich, J. S. Potaenko, O. F. Yakushko. 1972.
Biological productivity of different types of lakes,
p. 383-404. In Z. Kajak, A. Hillbricht-Ilkowska
(ed.). Productivity problems of freshwaters.
PWN-Polish Scientific Publishers, Warsaw.

APPENDICES

Appendix 1

Estimation of Tag Loss

The detachment of a mark produces gross overestimates of abundance in all mark and recapture estimates but is infrequently evaluated. This problem was briefly examined by Beverton and Holt (1967, p.204ff) and Gulland (1963). Robson and Regier (1966) present a comprehensive model with appropriate tests but require a permanent mark. In this study double tagging was examined and since no individual lost both marks the latter model applied.

Tag loss is assumed to occur proportionally to the number remaining attached. The appropriate maximum likelihood estimator of r , the tag retention coefficient is:

$$\sum_j \frac{(X_j - n_j \hat{r}^{t_j}) t_j}{1 - \hat{r}^{t_j}} = 0$$

X_j = no. of tag retentions in a sample of n fish

n_j = no. of fish samples

r = probability that a tagged fish retains its tags over one month

t_j = time in months.

Fish bearing two tags were released in May and June of 1975 and recaptured during June, August, and September.

The homogeneity of the two possible estimates of 2 month retention rate, \hat{r}^2 , is tested in the 2 x 2 contingency table:

	May-August	June-September	Total
Tag Retained	9	14	23
Tag Lost	8	8	16
Total	17	22	39

yielding a chi-square value of χ^2_1 d.f. = .4534 with $P > .50$.

Since homogeneity isn't rejected the maximum likelihood estimate is calculable using the pooled data in the form:

	$t_1 = 1$	$t_2 = 2$	$t_3 = 3$	$t_4 = 4$
n_j	26	28	39	18
X_j	24	18	23	12

The iterative solution for \hat{r} equals .857

$$\hat{\sigma}_r = .857 / \sqrt{3362.37} = .0148$$

Thus, the 95% confidence interval is $.828 < \hat{r} < .886$.

The chi-square goodness-of-fit statistics is now computed from:

$$\chi^2 = \sum_j \frac{(X_j - n_j \hat{r} t_j)^2}{n_j \hat{r} t_j (1 - \hat{r} t_j)}$$

$$\chi^2_3 \text{ d.f.} = .9252 + 1.207 + .265 + 1.171 = 3.568$$

which is not significant ($P \approx .40$).

The overall test of the model is also non-significant ($P = .45$) so we may presume that the model adequately describes the tag loss phenomenon over the summer of 1975. Since we have two loseable tags \hat{r} actually estimates \hat{r}^2 so \hat{r} is a maximum likelihood estimator with a value of .926, and tag retention is 93% which is the value used in subsequent tabulations.

Cucin and Regier (1965) present an application of the above model. Tag loss is assumed to be a constant exponential function

$$\frac{X_0 - X_t}{X_0} = e^{-\pi t} = \hat{r}$$

Therefore π is .0769 and the corrected number of recaptures will be approximated by

$$\tilde{R}_i = R_i e^{\pi (t_1 - t_0)}$$

and yield the corrected abundance estimates

$$\tilde{N}_i = \frac{(M_i + 1) (C_{i+1} + 1)}{(\tilde{R}_{i+1} + 1)}$$

where M_i = no tagged animals released at time i

C_{i+1} = no individuals captured at time $i+1$

R_{i+1} = corrected number of individuals recaptured at time $i+1$.

It was assumed that tag loss did not occur during winter so no correction was applied to fall estimates.

References for Appendix 1

- Beverton, R. J. H. and Holt, J. J. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II Mar. Fish. B. G. Minist. Agric. Fish. Food. 19:533 pp.
- Cucin, D., and H. A. Regier. 1965. Dynamics and exploitation of lake whitefish in southern Georgian Bay. J. Fish. Res. Board Can. 23:221-274.
- Gulland, J. A. 1963. On the analysis of double-tagging experiments. Int. Comm. Northwest Atl. Fish. Spec. Publ. 4:228-229.
- Robson, D. S. and H. A. Regier. 1966. Estimates of tag loss rates from recoveries of fish tagged and permanently marked. Trans. Am. Fish. Soc. 95:56-59.

Appendix 2. Chapman (1952) estimates of population size both corrected and uncorrected for tag loss based on an exponential tag loss model.

Date ^b	Number of Fish			Population Estimate	Months since tagging	Corrected Recapture \tilde{R}_j	Corrected Population Estimate (\tilde{N})	Standard Error \tilde{N}
	Captured C_j	Marked M_j	Recaptured R_j					
1972								
May 24	143	114	-	9200	-	-	9200	28363
June 30	79	72	0	1205	1.23	.00	1169	1571
July 22	32	20	1	2562	.73	1.06	2562	8270
Sept.16	121	121	0	2338 ^a	1.80	.00	2338 ^a	1183
1973								
May 20	114	102	5	5099	-	5.00	4926	6416
June 16	98	86	1	5090	.90	1.07	4965	6536
July 14	116	103	1	6864	.60	1.05	6568	8444
Aug.16	131	109	1		1.10	1.09	12210	37492
Sept.14	110	108	0		.97	.00	13298	40795
1974								
May 26	121	102	0	4197 ^a	-	.00	4007 ^a	2675
June 19	162	87	3	4708	.80	3.19	4359	5432
Aug.16	106	100	1	3299	1.93	1.16	3132	2682
Sept.15	97	97	2	1927 ^a	1.00	2.16	1927 ^a	617
1975								
May 18	235	235	11	2460 ^a	-	11.00	22284 ^a	450
June 17	270	231	25	2952 ^a	1.00	27.00	2602 ^a	610
Aug. 8	228	191	17	4128 ^a	1.73	19.42	3522 ^a	1140
Sept.4	214	214	10	-	.90	10.72	-	-

^a Estimates unbiased based on criteria of Robson and Regier (1964).

^b Refer to midpoint of sampling period.

Appendix 3. Estimation of Annual Mortality by the Catch Curve Analysis of Robson and Chapman (1961).

Robson and Chapman (1961) demonstrated that given similar rates of recruitment and survival for individual year-classes the annual mortality was estimable from the age-frequency distribution in the catch.

1972	Age	Coded Age	Number in the catch
	2+	0	$N_0 = 12$
	3+	1	$N_1 = 9$
	4+	2	$N_2 = 4$
	5+ and older	3 and older (K+1)	$m = 351$

Total sample size, $n = 376$

$$T = N_1 + 2N_2 + 3N_3 + \dots + m(K+1)$$

$$= 9 + 2(4) + 3(351) = 1070$$

$$\text{Annual Survival Estimate} = \frac{T}{n - m + T} = \frac{1070}{376 - 351 + 1070} = \frac{1070}{1098} = .977$$

$$\text{Heincke's estimate} = \frac{n - N_0}{n} = \frac{376 - 12}{376} = \frac{364}{376} = .989$$

To test whether the difference in estimates is the result of sampling error

$$\begin{aligned} \text{Chi square with 1 d.f.} &= \frac{(\text{Best est.} - \text{Heincke's est.})^2}{\frac{T(T-1)(n-1)}{n(n+T-1)^2(n+T-2)}} \\ &= .38059 < 3.841 = \chi^2_{\alpha} = .05 \end{aligned}$$

Thus χ^2 is not significant and the model appropriate.

Variances for the estimate are obtained from

$$\frac{s(1-s)^2}{n(1-s^3)} = \frac{.000516}{25.352} = .00002$$

The identical procedure was repeated for 1973-1975 data to obtain estimates of annual survival (Table 8).

References for Appendix 3

Robson, D. S. and D. G. Chapman. 1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181-189.

Appendix 4. Seasonal change in weight and instantaneous growth rates ($\bar{g\dot{w}}$) based on weights (\bar{w}) predicted from weighted linear regression equations fitted to observed weights (\bar{w}). (Sample size in parenthesis).

		1974				
		May 26 ^a	June 19	Aug. 16	Sept.16	Regression Equation
1966	\bar{w}	987(6)	1077(3)	1362(5)	1113(4)	$\frac{\Delta}{w} = 703.92 + 2.163t^b$
	$\frac{\Delta}{w}$	1018	1077	1197	1264	$F_{1,2d.f.} = 1.524$
	$\bar{g\dot{w}}$.0517	.1106	.0545		
1967	\bar{w}	667(90)	674(71)	773(54)	802(46)	$\frac{\Delta}{w} = 473.293 + 1.277t$
	$\frac{\Delta}{w}$	658	690	764	804	$F_{1,2} = 55.561^{*c}$
	$\bar{g\dot{w}}$.0473	.1019	.0505		
1968	\bar{w}	599(1)	---	544(1)	684(2)	$\frac{\Delta}{w} = 475.23 + .6839t$
	$\frac{\Delta}{w}$	575	---	631	652	$F_{1,2} = .3930$
	$\bar{g\dot{w}}$	---	---	.0330		
1969	\bar{w}	---	464(3)	551(2)	576(2)	$\frac{\Delta}{w} = 244.772 + 1.302t$
	$\frac{\Delta}{w}$	---	466	542	582	$F_{1,2} = 66.477^*$
	$\bar{g\dot{w}}$	---	.1502	.0719		
1970	\bar{w}	350(1)	411(3)	337(1)	652(1)	$\frac{\Delta}{w} = 141.87 + 1.578t$
	$\frac{\Delta}{w}$	371	410	502	551	$F_{1,2} = 1.544$
	$\bar{g\dot{w}}$.1011	.2014	.0930		
1971	\bar{w}	213(4)	219(11)	303(1)	372(2)	$\frac{\Delta}{w} = 1.448t - 17.752$
	$\frac{\Delta}{w}$	192	228	312	357	$F_{1,2} = 26.889^*$
	$\bar{g\dot{w}}$.1725	.3131	.1343		
1972	\bar{w}	60(14)	67(75)	165(37)	206(35)	$\frac{\Delta}{w} = 1.495t - 180.66$
	$\frac{\Delta}{w}$	36	74	160	207	$F_{1,2} = 97.05^*$
	$\bar{g\dot{w}}$.7101	.7791	.2541		

a Dates refer to midpoint of the sampling period.

b Time in days since the beginning of the year.

c Slope of the equation significantly different from zero at the .05 probability level.

Appendix 4. Seasonal change in weight and instantaneous growth rates ($\bar{g\bar{w}}$) based on weights (\bar{w}) predicted from weighted linear regression equations fitted to observed weights (\bar{w}). (Sample size in parenthesis).

		1975				
		May 18 ^a	June 17	Aug. 8	Sept. 4	Regression Equation
1966	\bar{w}	1126(16)	1167(8)	1189(4)	1482(2)	$\frac{\Delta}{\bar{w}} = 847.2 + 1.966t$
	$\frac{\Delta}{\bar{w}}$	1117	1177	1280	1335	$F_{1,2} = 3.781$
	$\bar{g\bar{w}}$.0531	.0832	.0421		
1967	\bar{w}	792(167)	817(135)	903(61)	898(86)	$\frac{\Delta}{\bar{w}} = 645.32 + 1.0596t$
	$\frac{\Delta}{\bar{w}}$	791	823	879	908	$F_{1,2} = 35.982^*$
	$\bar{g\bar{w}}$.0407	.0647	.0332		
1968	\bar{w}	613(1)	762(1)	783(2)	642(1)	$\frac{\Delta}{\bar{w}} = 614.71 + .5131t$
	$\frac{\Delta}{\bar{w}}$	685	701	728	742	$F_{1,2} = .1699$
	$\bar{g\bar{w}}$.0229	.0373	.0195		
1969	\bar{w}	613(8)	580(5)	586(2)	736(3)	$\frac{\Delta}{\bar{w}} = 480.02 + .81525t$
	$\frac{\Delta}{\bar{w}}$	592	617	659	682	$F_{1,2} = 1.4123$
	$\bar{g\bar{w}}$.0418	.0664	.0340		
1970	\bar{w}	602(2)	555(4)	688(2)	711(2)	$\frac{\Delta}{\bar{w}} = 367.67 + 1.358t$
	$\frac{\Delta}{\bar{w}}$	554	596	666	704	$F_{1,2} = 4.430$
	$\bar{g\bar{w}}$.0733	.1119	.0555		
1971	\bar{w}	334(1)	384(6)	533(3)	481(1)	$\frac{\Delta}{\bar{w}} = 54.955 + 2.0037t$
	$\frac{\Delta}{\bar{w}}$	329	392	496	552	$F_{1,2} = 9.8007$
	$\bar{g\bar{w}}$.1727	.2359	.1072		
1972	\bar{w}	215(32)	219(106)	314(127)	350(97)	$\frac{\Delta}{\bar{w}} = 1.4722t - 14.6312$
	$\frac{\Delta}{\bar{w}}$	187	233	309	350	$F_{1,2} = 45.476^*$
	$\bar{g\bar{w}}$.2183	.2844	.1251		
1973	\bar{w}	---	92(6)	192(12)	210(10)	$\frac{\Delta}{\bar{w}} = 1.4923t - 146.599$
	$\frac{\Delta}{\bar{w}}$	---	104	182	223	$F_{1,2} = 8.5091$
	$\bar{g\bar{w}}$	---	.5569	.2069		

a Dates refer to midpoint of the sampling period.

Appendix 5. Analysis of Covariance on the total length-scale radius relationship for individuals sampled during 1972-1975. I. Bartlett's test for Homogeneity of Variance.

Year	Sum of Squares $f_i s_i^2$	Degrees of Freedom f_i	Mean Squares f_i^2	$\text{Log } e^{s_i^2}$	$f_i \text{Log } e^{s_i^2}$	Reciprocals ($1/f_i$)
1972	33.647	418	.0806	-2.520	-1053.180	.0024
1973	49.428	587	.0842	-2.475	-1452.537	.0017
1974	51.116	482	.1061	-2.244	-1081.530	.0021
1975	57.860	946	.0612	-2.794	-2643.330	.0011
a=4	192.061	2433			-6230.577	.0073

$$\chi_{(a-1)}^2 \text{d.f.} = \frac{M}{C} \left[\frac{(\sum f_i) \log e \bar{s}^2 - \sum f_i \log e s_i^2}{1} + \frac{1}{3(a-1)} \left[\sum \frac{1}{f_i} - \frac{1}{\sum f_i} \right] \right]$$

$$\bar{s}^2 = \frac{\sum f_i s_i^2}{\sum f_i} = \frac{192.051}{2433} = .0789$$

$$M = [(2433 \times -2.539) - (-6230.579)] = 52.897$$

$$C = 1 + \frac{1}{3(3)} \left[.0073 - \frac{1}{2433} \right] = 1.0008$$

$$\chi_{3\text{d.f.}}^2 = \frac{52.897}{1.0008} = 52.857^{***} > 12.84$$

Reject H_0 : that the variances are homogeneous.

Appendix 6. Back-calculated lengths (mm) at annulus formation for West Blue Lake walleye, 1972-1975. N refers to sample size.

Year Class	N	AGE									Date Collected
		1	2	3	4	5	6	7	8	9	
1963	3	156	293	393	457	493	519	530	539	-	May 1972
1964	4	138	267	357	415	447	465	475			May 1972
	4	140	280	370	434	467	488	499	505		June 1972-June 1973
1965	3	131	251	374	413	453	477				May 1972
	6	121	241	326	395	414	433	445			June 1972-June 1973
	4	134	254	360	431	471	501	521	529		July 1973-June 1974
	1	148	290	400	487	529	568	586	594	601	Aug. 1974-June 1975
1966	4	124	232	305	357	397					May 1972
	21	129	241	320	374	405	425				July 1973-June 1974
	25	136	255	336	392	424	446	458			July 1973-June 1974
	33	128	253	343	405	440	464	478	488		Aug. 1974-June 1975
	6	113	233	332	402	443	473	488	499	508	Aug. 1975-Sept. 1975
1967	132	94	183	259	316						May 1972
	368	100	190	265	322	360					June 1972-June 1973
	446	107	197	273	328	365	392				July 1973-June 1974
	402	95	188	268	328	368	400	421			Aug. 1974-June 1975
	147	95	190	272	333	375	406	429	450		Aug. 1973-Sept. 1975
1968	5	85	171	237	288						June 1972-June 1973
	6	110	197	269	324	354					July 1973-June 1974
	6	107	206	286	339	377	405				Aug. 1974-June 1975
	3	93	198	276	331	363	391	416			Aug. 1975-Sept. 1975
1969	3	111	212								May 1972
	11	96	219	287							June 1972-June 1973

Appendix 6. Back-calculated lengths (mm) at annulus formation for West Blue Lake walleye, 1972-1975. N refers to sample size.

Year Class	N	AGE									Date Collected
		1	2	3	4	5	6	7	8	9	
1969	17	104	224	291	333						June 1973-June 1974
	17	95	217	283	336	372					Aug. 1974-June 1975
	5	90	216	286	333	369	404				Aug. 1975-Sept. 1975
1970	2	140									May 1972
	20	121	238								June 1972-June 1973
	24	124	234	295							July 1973-June 1974
	8	122	239	304	351						Aug. 1974-June 1975
	4	110	235	312	363	402					Aug. 1975-Sept. 1975
1971	14	97									June 1973-June 1975
	23	107	224								July 1973-June 1974
	10	96	221	292							Aug. 1974-June 1975
	4	100	218	293	356						Aug. 1975-Sept. 1975
1972	111	81									July 1973-June 1974
	210	77	191								Aug. 1974-June 1975
	224	70	182	280							Aug. 1975-Sept. 1975
1973	12	103									Aug. 1974-June 1975
	22	101	220								Aug. 1975-Sept. 1975
1974	23	99									Aug. 1975-Sept. 1975

Appendix 7. Relative (h) and instantaneous (g) daily growth in length and weight from the last annulus (N refers to sample size).

Year	Class	1974				1975			
		May 26	June 19	Aug. 16	Sept. 15	May 18	June 17	Aug. 8	Sept. 4
1966	N	6	3	5	4	16	7	4	2
	h _L	.0091	.0155	.0099	.0154	.0134	.0166	.0087	.0062
	h _w	.0286	.0467	.0322	.0479	.0398	.0509	.0280	.0207
	g _L	.00026	.00028	.00017	-.00001	.00011	.00017	-.00009	
	g _w	.00073	.00064	.00051	-.00003	.00035	.00139	-.00026	
1967	N	90	71	54	46	167	132	61	86
	h _L	.0461	.0460	.0362	.0426	.0468	.0436	.0152	.0145
	h _w	.1495	.1569	.1181	.1393	.0121	.1411	.0488	.0456
	g _L	.00000	.00060	.00020	.00002	-.00010	.00041	-.00003	
	g _w	.00027	.00230	.00061	.00005	-.00035	.00158	-.00011	
1968	N	1	---	1	2	1	2	2	1
	g _L	.0364	---	.0438	.0500	.0769	.0416	.0388	.0229
	g _w	.1199	---	.1451	.1668	.2641	.1333	.1285	.0744
	g _L	---	---	.00019	.00010	-.00111	.00083	-.00057	
	g _w	---	---	.00061	.00033	-.00364	.00271	-.00182	
1969	N	---	3	2	2	8	5	2	3
	h _L	---	.0872	.0690	.0816	.0722	.0892	.0298	.0381
	h _w	---	.0003	.2347	.2816	.2448	.3109	.0969	.1249
	g _L	---	.00161	.00038	-.00004	.00052	.00084	.00030	
	g _w	---	.00970	.00120	-.00012	.00173	.00273	.00093	
1970	N	1	3	1	1	2	4	2	2
	h _L	.1216	.1489	.1188	.0874	.1073	.1231	.0509	.0558
	h _w	.4375	.5508	.4264	.3035	.3817	.4455	.1678	.1873
	g _L	.00100	.00224	-.00092	.00007	.00077	.00078	.00017	
	g _w	.00316	.00709	-.00271	.00024	.01168	.00250	.00061	
1971	N	4	8	1	2	1	6	3	1
	h _L	.3130	.2816	.1643	.1369	.2003	.1985	.0712	.1149
	h _w	1.3591	1.1366	.6178	.4939	.7813	.7620	.2430	.4108
	g _L	-.00101	.00315	-.00077	.00022	-.00005	.00151	.00148	
	g _w	-.00413	.01040	-.00220	.00072	-.00036	.00494	.01020	
1972	N	14	71	37	35	37	104	127	97
	h _L	1.6813	1.3660	.4455	.4681	.5005	.5215	.1732	.2045
	h _w	18.9917	11.9530	2.0829	2.1891	2.4962	2.6438	.6462	.7793
	g _L	-.00558	.00784	.00050	.00009	.00046	.00331	.00097	
	g _w	-.01804	.02662	.00109	.00038	.00138	.01128	.00288	

Appendix 8. Production estimates based on the arithmetic approach and growth rates determined from weights predicted from linear regression equations.

Date	Year Class	Mean Weight w (g)	Inst. Growth G	Abundance N	Biomass B (kg)	Mean Biomass \bar{B}	Production P (kg)	Annual Production (kg)
June 19	1966	1072		63	67.54			
	1967	690		1428	985.32			
	1968	-		-	-			
	1969	466		63	29.36			
	1970	410	.11070	63	25.83	156.46	17.32	
	1971	228	.10188	168	38.30	1336.88	136.20	
	1972	74	-	1470	108.73	-	-	
Aug. 16			.15017			36.90	5.54	
	1966	1197	.20143	205	245.39	23.21	4.67	
	1967	764	.31313	2210	1688.44	25.25	8.00	
	1968	631	.77912	41	25.84	175.59	136.81	
	1969	542		82	44.44	1754.59	308.54	
	1970	502		41	20.58			
	1971	312	.05450	41	12.79	196.64	10.72	
	1972	160	.05046	1515	242.40	1384.11	69.84	
	1973	65	.03304	123	8.00	31.84	1.05	
Sept. 15			.07188			39.10	2.81	
	1966	1264	.09304	117	147.89	18.28	1.70	
	1967	804	.13426	1343	1079.77	16.75	2.25	
	1968	652	.25407	58	37.82	223.98	56.91	
	1969	582	.01237	58	33.76	9.56	3.55	
	1970	551		29	15.98	1920.26	148.83	
	1971	357	-.12363	58	20.71	144.32	-17.84	
	1972	207	-.01630	993	205.55	1058.78	-17.26	
	1973	95	.04791	117	11.12	21.65	1.04	
May 18			.01704			35.53	.61	
	1966	117	.00543	126	140.74	12.42	.07	
	1967	791	-.08168	1312	1037.79	11.67	-.95	
	1968	685	-.10161	8	5.48	125.54	-12.76	
	1969	592	-	63	37.30	-	-	
	1970	554		16	8.86	1409.91	47.09	
	1971	329		8	2.63			
	1972	187	.05314	244	45.63	102.15	5.43	
	1973	-	.04072	-	-	934.92	38.07	
			.02295			7.99	.18	
			.04182			30.68	1.28	
			.07327			13.67	1.00	
		.17272			10.33	1.78		
		.21851			115.43	25.20		
					1215.17	72.94		

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Appendix 8. Production estimates based on the arithmetic approach and growth rates determined from weights predicted from linear regression equations.

Date	Year Class	Mean Weight \bar{w} (g)	Inst. Growth G	Abundance \hat{N}	Biomass B (kg)	Mean Biomass \bar{B}	Production P (kg)	Annual Production (kg)
June 17	1966	1177		54	63.56			
	1967	823		1011	832.05			
	1968	701		15	10.52			
	1969	617		39	24.06			
	1970	596		31	18.48			
	1971	392	.08325	46	18.03	65.06	5.42	
	1972	233	.06479	795	185.24	756.64	49.02	
	1973	92	.03736	46	4.23	14.77	.55	
Aug. 8	1966	1280	.06645			20.60	1.37	
	1967	879	.11199	52	66.56	17.90	2.00	3.73
	1968	727	.23593	775	681.23	18.67	4.41	119.67
	1969	659	.28442	25	18.90	348.16	99.02	2.82
	1970	666	.55698	26	17.13	17.84	9.94	6.07
	1971	496		26	17.32	125.966	171.73	4.77
	1972	309		39	19.34			7.49
	1973	199		1654	511.09			168.37
								13.49
								Aug.1974-Aug.1975 $\Sigma P = 346.41$

Appendix 9. Production estimates based on the arithmetic approach and growth rates back-calculated from scale samples.

Date	Year Class	Mean Weight \bar{w} (g)	Inst. Growth G	Abundance \hat{N}	Biomass (kg)	Mean Biomass \bar{B} (kg)	Production P (kg)	Annual Production (kg)
1974	1966	1077		63	67.85			
June 19	1967	674		1428	962.47			
	1968	-		-	-			
	1969	464		63	29.23			
	1970	411	.03712	63	25.89	173.53	6.441	
	1971	219	.13340	168	36.79	1335.40	178.142	
	1972	67	-	1470	98.49	-	-	
			.56260		1220.72	37.21	20.934	
			.41122			19.86	8.167	
Aug. 16	1966	1362	.60320	205	279.21	24.61	14.845	
	1967	743	1.54396	2210	1708.33	174.23	269.004	
	1968	544		41	22.30	1764.84	497.534	
	1969	551		82	45.18			
	1970	337		41	13.82			
	1971	303	.01530	41	12.42	204.72	3.132	
	1972	165	.01830	1515	249.98	1392.71	25.487	
	1973	65	.01830	123	8.00	30.99	.567	
			.03600		2339.24	39.30	1.415	
			-.08100			16.36	-1.325	
Sept. 15	1966	1113	-.06600	117	130.22	16.70	-1.102	
	1967	802	.03270	1343	1077.09	227.27	7.432	
	1968	684	.46659	58	37.67	9.56	4.461	
	1969	576		58	33.41	1753.36	40.066	
	1970	652		29	18.91			
	1971	372	-.00735	58	21.58	73.78	-.542	
	1972	206	.01225	993	204.59	1058.10	12.962	
	1973	95	.08085	117	11.12	22.29	1.802	
			-.02940		1536.59	36.01	-1.059	
			.05880			14.31	.841	
			.17640			12.12	2.138	
			.09310			128.62	11.975	
						-	-	
						1344.81	28.117	

Appendix 9. Production estimates based on the arithmetic approach and growth rates back-calculated from scale samples.

Date	Year Class	Mean Weight \bar{w} (g)	Inst. Growth G	Abundance N	Biomass (kg)	Mean Biomass \bar{B} (kg)	Production P (kg)	Annual Production (kg)	
1975	1966	1126		126	141.88				
May 18	1967	792		1312	1039.10				
	1968	613		8	4.90				
	1969	613		63	38.62				
	1970	607		16	9.71				
	1971	334	.01050	8	2.67	102.45	1.076		
	1972	215	-.01050	244	52.46	932.55	-9.792		
	1973	-	-.10920	-	-	8.17	-.892		
			.05190			1289.34	30.62	1.589	
June 17	1966	1167	-.01080	54	53.02	13.46	4.716		
	1967	817	.04140	1011	825.99	10.17	-.110		
	1968	762	-	15	11.43	113.28	4.690		
	1969	580		39	22.62	-	-		
	1970	555		31	17.21	1210.70	1.277		
	1971	387	.07228	46	17.66	62.42	4.512		
	1972	219	.08216	795	174.11	762.91	62.681		
	1973	92	.14092	46	4.23	16.87	2.377		
			.14196			1136.27	18.93	2.687	
			.13000			17.55	2.282		
Aug. 8	1966	1189	.25688	52	61.83	19.23	4.940	8.178	
	1967	903	.58656	775	669.83	350.87	205.806	91.338	
	1968	783	.69500	26	20.36	17.84	12.340	3.854	
	1969	586		26	15.24	1266.62	297.683	4.632	
	1970	688		26	17.89			6.514	
	1971	533		39	20.79			5.866	
	1972	319		1654	527.63			229.903	
	1973	199		158.	31.44			16.801	
					1383.74	Aug.1974-Aug.1975 $\Sigma P = 367.086$			