Migration and population dynamics of the Peace–Athabasca Delta goldeye population

by D. B. Donald and A. H. Kooyman

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SK 471 C 33 No. 31 ¹Limnos Associates (Calgary), Calgary, Alta. Present address: CWS, Dept. of Biology, Univ. of Calgary, Calgary, Alta. T2N 1N4 ²CWS, Winnipeg, Man. R3T 2N6



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Abstract

Goldeye (*Hiodon alosoides*) begin moving into the Peace-Athabasca Delta area in March, but do not enter the delta lakes until after breakup in the Peace River in May. Mature goldeye spawn in the delta lakes primarily between the middle and the end of May. Goldeye of all ages begin migrating from the delta in July. The peak migration period for yearling and older goldeve is from mid-July to mid-August. The majority of adult goldeye return to the Peace River by the end of August, but some young remain in the delta until at least early December. All of these goldeye winter in the Peace River, probably throughout the lower 150-250 km. The distance from the wintering areas in the Peace River to the delta and back can be as much as 700-800 km for some fish.

The eggs of goldeye hatch in early June and mortality of the larvae is high during that month, but for the rest of the summer numbers remain relatively constant. In the Mamawi-Claire Lake system, young-of-the-year goldeye are most abundant in Mamawi Lake and along the north and west shores of Lake Claire, but the relative abundance in these locations varies from year to year. Young-of-the-year goldeye are found within a few hundred metres of the shoreline in these lakes, showing a clumped distribution.

Between 1971 and 1974, year-class strength was highly unbalanced. The 1964, 1965 and 1971 year-classes were by far the most abundant fish in the population. Goldeye in the 1970's were larger than in 1947–48 and 1954. The unusual year-class abundances and growth rates in the early 1970's are attributed to over-harvest of this population by the 1948–66 commercial fishery, and not to unusually low water levels in the delta between 1968 and 1971. Between 1971 and 1973 females comprised from 17 to 23% of the adult stock, but in other years the sex ratio

was much closer to one to one. The natural mortality of the adult stock was about 51% and recruitment was negligible for 2 years in the early 1970's. The numbers of adult fish which entered the delta in 1972, 1973 and 1974 were 100 500, 37 000 and 18 000 respectively, and were considerably less than the numbers of adult fish in the 1940's and 1950's when there were probably between 350 000 and 1 300 000 fish in this population. The adult stock will recover in numbers in 1977 and 1978, the years when the 1971 year-class of goldeye are 6 and 7 years old.

Résumé

La laquaiche aux veux d'or (Hiodon alosoides) commence à arriver en mars dans le secteur du delta Paix-Athabasca, mais elle ne pénètre dans les lacs du delta qu'après le dégel de la rivière de la Paix en mai. Les adultes fraient dans les lacs du delta, surtout entre le milieu et la fin de mai. Bien que la migration hors du delta commence en juillet, la période de pointe tant pour les petits d'un an que pour les plus âgés ne survient qu'entre la mi-juillet et la mi-août. La plupart des adultes retournent à la rivière de la Paix fin août, mais il reste des petits dans le delta au moins jusqu'au début de décembre. Toutes ces laquaiches hivernent dans la rivière de la Paix, probablement dans les 150 à 250 derniers kilomètres de son cours. L'aller-retour de l'aire d'hivernage de la rivière de la Paix au delta peut, pour certaines laquaiches, comporter un trajet de 700 ou même 800 kilomètres.

Les œufs de la laquaiche aux yeux d'or éclosent début juin; le taux de mortalité des larves est élevé ce mois là, quitte à ce que l'effectif en demeure relativement constant le reste de l'été. Pour ce qui est du bassin des lacs Mamawi et Claire, les petits de l'année sont plus nombreux dans le lac Mamawi et le long des rives nord et ouest du lac Claire, mais leur abondance relative y varie d'une année à l'autre. Les petits de l'année se trouvent à quelques centaines de mètres tout au plus du rivage de ces lacs et ils présentent une distribution compacte.

Entre 1971 et 1974, la rapport de la cohorte des petits de l'année à la population totale manifestait un déséquilibre très marqué. En 1964, 1965 et 1971, la cohorte des petits de l'année était de loin la plus nombreuse de toute la population. Les laquaiches étaient, à compter de 1970, de plus grande taille qu'en 1947-48 et en 1954. C'est à la pêche commerciale abusive pratiquée de 1948 à 1966 et non pas à quelque influence néfaste du niveau anormalement bas des eaux du delta entre 1968 et 1971 qu'on attribue tant l'effectif élevé des cohortes de petits de l'année que le taux de croissance tous deux inhabituels, observés peu après 1970. Entre 1971 et 1973, les femelles constituaient de 17 à 23% de la population adulte mais, les autres années, le rapport des sexes était bien plus près de l'unité. Pendant deux ans, au début de la présente décennie le taux de mortalité naturelle a atteint environ 51% chez la population adulte tandis qu'était négligeable le renouvellement. Le nombre des poissons adultes à pénétrer dans le delta en 1972, 1973 et 1974 était respectivement de 100 500, 37 000 et 18 000, soit bien moins que l'effectif des poissons adultes chez la population lors des décennies de 1941 et de 1951 pendant lesquelles les pêcheurs commerciaux en prélevaient souvent un poids total de plus de 45 000 kg par an. L'effectif des adultes se rétablira cependant en 1977 et 1978, alors que les sujets de la cohorte née en 1971 auront 6 ou 7 ans.

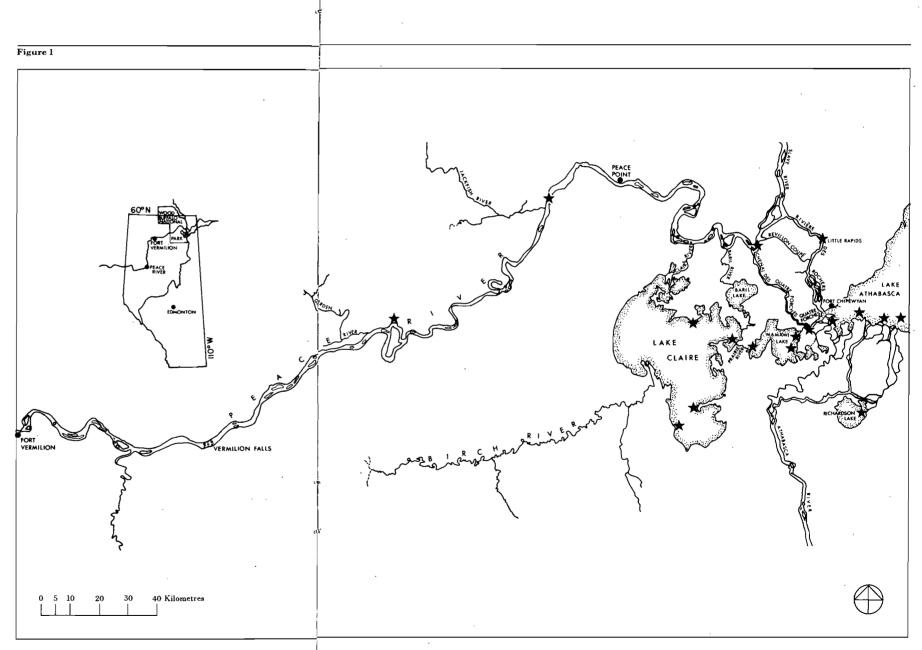
Introduction

Figure 1
Map of the study area. Locations where goldeye tagged at Quatre Fourches were recovered are shown by stars

Between 1948 and 1966 a commercial fishery operated in the Mamawi Lake, Prairie River and Lake Claire areas (Fig. 1) of the Peace—Athabasca Delta. During these years the fishery produced approximately 30% of the North American commercial catch of goldeye (*Hiodon alosoides*). During the first 3 years of operation, the average annual catch was 65 455 kg, declining to an average annual catch of 11 136 kg during the last 4 years (Table 1). The fishery collapsed in 1966, and commercial fishing for goldeye was discontinued in the Mamawi-Claire Lake system.

In the fall of 1971 a temporary dam was built at Quatre Fourches (Fig. 1) to increase water levels in the Mamawi-Claire Lake system. Low water levels had existed in the delta since 1968 when the W.A.C. Bennett Dam and Shrum Generating Station were completed on the upper Peace River in British Columbia (Townsend 1975). The low water levels caused major changes in the plant communities of the delta (Dirschl 1972), and had deleterious effects on waterfowl populations (Nieman and Dirschl 1973). There was reason to believe that the dam at Quatre

Table 1	
Goldeye harvest records for Lake Claire*	
Year	Harvest (kg)
1948	53 978
1949	108 863
1950	32 389
1951-53	(Operations suspended)
1954	108 863
1955	(Not fished)
1956	79 991
1957	60 336
1958 .	(Not fished)
1959	64 064
1960	46 339
1961	42 494
1962	46 686
1963	9 979
1964	658
1965	21 254
1966	12 509



Four ches and the low water levels could affect delta fish populations.

Between 1971 and 1975 the goldeye of the Peace–Athabasca Delta were studied in order to assess the status of the population. The study was designed to obtain an estimate of population size and an understanding of migration, home range, growth rates, and feeding habits. Kennedy and Sprules (1967) and Donald and Kooyman (1974) have described the feeding habits of goldeye in the Peace–Athabasca Delta and the subject will not be discussed further in this book. A report dealing with the preliminary aspects of this study was presented by Kooyman (1973).

The Peace-Athabasca Delta is formed at the confluence of the Peace and Athabasca rivers (Fig. 1), and is situated largely in Wood Buffalo National Park. The Peace and Athabasca rivers have an average annual flow of 1988 m³/s and 772 m³/s respectively. Lake Claire and Mamawi Lake, two of the delta's four large lakes, are of major importance to goldeye. Lake Claire, approximately 1456 km², is seldom more than 3 m deep even at highest water levels in spring during years when there is overland flooding from the Peace and Athabasca rivers. The average annual water depth for Lake Claire would be about 2 m in a typical year. In March of 1971 Lake Claire had a maximum depth of 1.5 m, and was frozen to the bottom over most of its area. Water beneath the ice was devoid of oxygen. Mamawi Lake, approximately 168 km², has a maximum depth of 1.5 m during flooding. In March 1971, when water levels were low, it had 46 cm of ice and was frozen to the bottom throughout its area. The above conditions indicate that fish can only remain in these lakes from May to mid-winter.

In this study goldeve were considered to be adult when 6 years old. They were caught in 9.5 and 10.2 cm (3¾ and 4 in.) stretch mesh multifilament nylon twine gill nets, 0.91 to 1.22 m deep and 45.7 m long. Juvenile goldeve were those which were 1-5 years old. They were sampled with survey nets 36.4 m long and 1.8 m deep, made up of four mesh sizes, 9.1 m each, of 3.8, 5.1, 7.6 and 10.2 cm stretch measure. The 1971 yearclass was sampled from July to November in 1972 and in May and June of 1973 with nets of one mesh size (3.8 cm), 22.8 m long and 2.4 m deep. Gill netting was carried out in Lake Claire, Prairie River, Mamawi Lake, Quatre Fourches, Lake Athabasca, Baril Lake, Baril River, Rivière des Rochers, Slave River, and the Peace River (Fig. 1). In these lakes and rivers the nets were set perpendicular to the shoreline and not more than 50 m from it.

Young-of-the-year goldeye (and yearling and 2-year-old goldeye caught in May and June) were collected by towing two 1-m² trawl nets, one on each side of a boat powered by an outboard motor. The nets were tapered to a point 160 cm from the square frame. A 2-min tow was made at each station with the motor at full throttle. Trawling was carried out 3–10 m from the bank in streams, and close to the shore (never more than 300 m from land) in lakes where water was 1.0–1.5 m deep.

In July and August of each year, samples of goldeye were collected with gill nets from the Mamawi-Claire Lake system. In 1974, they were collected in June and October from the upper Peace River near the towns of Peace River and Fort Vermilion. For each year and location samples ranged from 105 to 307 fish. These goldeye were weighed and measured fresh in the field. Scale samples were taken from below the dorsal fin of each fish and were dried for age determination in the laboratory. Sex was deter-

mined by anal fin shape in mature goldeye, and by examination of the gonads in juvenile goldeye. Sexual maturity was assessed by examining gonadal development and testing for the presence of ripe sexual products.

In order to determine the seasonal migrations of goldeye and the population dynamics of the adult stock, adult fish were either marked with coloured Floy tags or numbered spaghetti tags using a method described by Dell (1968), or they were fin-clipped. A total of 4375 goldeye, of which 480 were recaptured, were marked and released at Quatre Fourches during the study. Donald and Kooyman (1976) have discussed the merits of the tagging method in detail. Estimates of various population parameters were made by using mark-recapture data and Bailey's triple catch method or the Petersen method. The formulae for both methods were taken from Ricker (1975).

1. Distribution and migration of adult

Adult goldeye were first caught at Quatre Fourches during early March. Between March and break-up, three tagged goldeye were recovered by domestic fishermen in this area. These first catches indicated that during late winter some goldeye were moving into Chenal des Quatre Fourches from their wintering areas in the Peace River, although they could not enter the delta lakes, which were frozen to the bottom at this time of the year.

In the spring, shortly after break-up, goldeye which winter in the lower Peace River migrate into the Peace-Athabasca Delta to spawn (Fig. 2). During the study, break-up on the Peace River and Chenal des Quatre Fourches began during the last week of April and was essentially completed during the first week of May. Break-up in Mamawi Lake and Lake Claire was completed one to two weeks later than in the rivers and channels. The earliest and latest dates for the beginning and the end of migration at Quatre Fourthes were 4 May and 26 May. In 1972, the peak of the migration was on 21 May; in 1973 and 1974 it was on 11 May; and in 1975 it was on 14 May. The migration in 1972 was delayed because of construction of the dam at Quatre Fourches.

Tag recoveries on Rivière des Rochers during the spawning migration in 1974 and a spring survey for immature goldeye in Chenal des Quatre Fourches and Rivière des Rochers indicated that both rivers are used by large numbers of goldeye migrating into the Mamawi-Claire Lake system. A tag recovery from Richardson Lake in July 1973, and another in May 1974, indicated that the small population of goldeye which spawn in this lake also comes from the Peace River. The goldeye recovered in May had reached this location a maximum of 18 days after

being tagged at Quatre Fourches. Those fish which spawn in Richardson Lake migrate through Chenal des Quatre Fourches or Rivière des Rochers, Lake Athabasca, and the Athabasca River. Those which spawn in Baril Lake probably migrate into this lake through the Baril River, although it is possible that they could reach Baril Lake through a channel which joins this lake with Lake Claire.

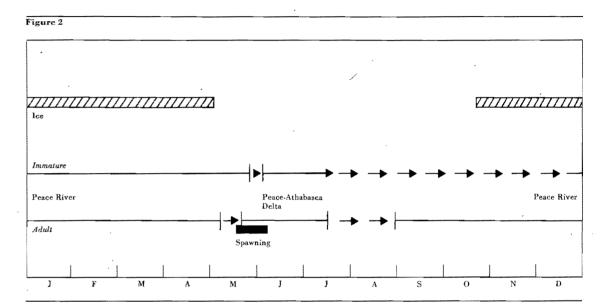
Gill net catches at Quatre Fourches showed that the majority, if not all, of the goldeye migrated into the delta after break-up and after ice had cleared from the Peace River. Therefore, the spring migration may be initiated by completion of these events followed by increasing water temperatures in the Peace River. The delay in the spring migration following break-up minimizes the chances of goldeye being stranded in inland lakes during years when flooding occurs, and also ensures that fish will have open water conditions in the large delta lakes which freeze to the bottom in the late winter of most years.

The migration from the Peace River to Quatre Fourches can be upstream or downstream depending on spring water levels or the channel used. During the study, the migration from Quatre Fourches into Mamawi Lake was upstream.

Before the end of May mature goldeye migrate through Mamawi Lake and Prairie River, and reach all the shoreline areas of Lake Claire. However, gill net catches in the Mamawi-Claire Lake system in late May and early June indicated that not all goldeye undertake the complete migration from Quatre Fourches to Lake Claire. Many fish remained in the Mamawi Lake and Prairie River area.

During June, July and August adult goldeye were found throughout the Peace-Athabasca Delta. Goldeye tagged at Quatre Fourches during the spawning migration were recaptured in

Figure 2
Diagrammatic representation of the seasonal distribution and migration of goldeye



Mamawi Lake, Prairie River, along the north, west, and east shores of Lake Claire, in the west end of Lake Athabasca, and in Richardson Lake. Catches of mature goldeye in the latter two lakes were very small in number compared with those from Mamawi Lake and Lake Claire.

Adult goldeye catches remained relatively low at Quatre Fourches throughout June and the first week of July, but increased thereafter, and reached peak numbers during the last week of July and the first week of August, indicating the summer migration to the Peace River was well underway. Catch records from Quatre Fourches and other stations throughout the delta indicated that this migration was essentially completed by the end of August (Fig. 2).

During late summer and fall, three tagged goldeye were recaptured near the junction of the Peace River and Chenal des Quatre Fourches (Fig. 1), and four were caught on the Peace River near the mouth of the Jackfish River (about 164 km from Quatre Fourches). Tagged goldeye were also reported from the Peace River near Garden River (about 257 km from Quatre Fourches).

A total of 46 goldeye were caught in the lower Peace River in the fall of 1973, of which three (6.5%) were tagged. It was determined that 5.8% of a much larger sample of 2123 goldeye, which were migrating from the Mamawi-Claire Lake system during the summer of 1973, had been tagged. The similarity of these two percentages suggests that most of the goldeye in the lower Peace River in September and October came from the Mamawi-Claire Lake system.

In 1974, no tagged goldeye were recovered from 154 adult goldeye caught in the Peace River downstream from the town of Peace River in June or from 113 adult goldeye collected near Fort Vermilion in October. There is an obvious

contrast between the above catches and the 12.4% tag recovery from 105 adult goldeve collected from the Peace-Athabasca Delta in July and August of 1974. The sample of goldeye taken near Fort Vermilion was collected upstream from the Vermilion Rapids and Falls (Fig. 1). These rapids are probably a difficult, but not an impassable, barrier to fish moving upstream. There is evidence that goldeve taken upstream from these rapids differ in their life history (see following section) from those taken in the lower Peace River. The proportion of tagged fish taken in the two locations also differs. This suggests that the Vermilion Rapids and Falls separate two distinct populations of goldeve.

A goldeve tagged at Cumberland Lake during a migration on the Saskatchewan River was recovered 4 days later, 177 km downstream at The Pas (Reed 1962). The Saskatchewan River, between Cumberland Lake and The Pas, is similar in size and current velocity to the lower Peace River. If it is assumed that goldeye can move 177 km downstream in 4 days, then goldeye wintering in the Peace River downstream from the Vermilion Falls could reach Chenal des Quatre Fourches within 7 or 8 days once the spring migration is underway.

Distribution and migration of juvenile goldeve

On 30 May 1972, large numbers of yearling goldeve were observed migrating into Mamawi Lake through a fishway at Quatre Fourches. There was no indication of any migration of young fish before this date. In late May of 1973, 52 trawl samples were taken in an area which included Lake Mamawi, Chenal des Quatre Fourches, Rivière des Rochers, Revillon Coupé, and Lake Athabasca. The young goldeve were concentrated near Quatre Fourches and in the Rivière des Rochers within a few miles of Lake

Athabasca, but had not reached Lake Mamawi. Young goldeye were migrating into Lake Mamawi by 31 May. These data indicate that the spring migration of juvenile goldeve follows the migration of adult goldeve by 1 or 2 weeks.

Juvenile goldeye were abundant throughout the Peace-Athabasca Delta, and the lower Peace River in the summer (Table 2). The best catches in 1973 were obtained from the Mamawi-Claire Lake system. The Slave River was the only area where juvenile goldeve were rare. Gill nets set in Lake Claire in November failed to yield any goldeve, although net catches at Quatre Fourches showed the outward migration continued until December. Thus, at least some juvenile goldeye

Table 2 Seasonal changes in the average number of juvenile goldeye caught in 1972* and 1973†

	Mean catch	Total	No. of	
	per station	hours	stations	
S	per hour	fished	sampled	Date
	e	Lake Clair	irie River and	1972 Mamawi Lake, Pr
37,26	40.33	9.75	6	July 16-23
10.91	15.86	8.33	7	Aug. 16-24
35.90	36.40	3.00	5 5	Sept. 6-17
43.56	32.00	2.55	5	Sept. 30-Oct. 5
9.96	5.75	4.00	4	Nov. 25-28
	e	Lake Claire	irie River and	1973 Mamawi Lake, Pr
3,12	3.99	142,33	6	June 5-July 1
2.91	3.95	108.75	7	July 3-18
2.87	3.48	20,75	6	Aug. 30-Sept. 1
0.48	1.24	92.50	4	Oct. 6-7
				1973 Lake Athabasca
0.52	0.52	60,00	2	June 22-24
0.39	0.93	78.50	2 3 2	Sept. 13-15
0.20	0.51	70,75	2	Oct. 17-27
0.00	0.00	4.25	I	Dec. 13
			rs	1973 Rivière des Roch
1,52	1.35	110.50	4	June 21-25
4.49	6.41	19.00	4	Aug. 29
				1973 Peace River
1.25	1.62	96,00	4	July 6-7
1.07	0.93	102.50	6	Sept. 18-Oct. 3
		River	Lake and Claire	1973 Baril River, Baril
4.58	6.20	10,00	3	Aug. 23-Sept. 5
				1973 Slave River
0.07	0.09	100.00	4	June 27-28
0.07	0.06	89.25	4	Sept. 11-12

remain in the delta well after most adult fish have returned to the Peace River (Fig. 2).

The main migration of juvenile and adult fish from the Mamawi-Claire Lake system back to the Peace River occurred after mid-July, a time when the flow direction in Prairie River, Chenal des Quatre Fourches and Rivière des Rochers was consistently toward the Peace River. Therefore the migration to the Peace River is a "downstream" movement of fish, but this becomes an "upstream" migration once the fish reach the Peace River.

3. Distribution of young-of-the-year goldeye

Observations during 3 years indicated that spawning in the Mamawi-Claire Lake system began approximately in mid-May and was essentially completed by the end of May, although a few fish spawned as late as mid-June. Apparently most spawning occurred over a 5-7 day period. Kennedy and Sprules (1967) noted that goldeye spawn in May or June, and that spawning continues for 3-6 weeks. Goldeve larvae were first collected on 4 June 1972 and on

1 June 1973. On these dates the larvae were similar in appearance to the pro-larvae described by Battle and Sprules (1960), which indicated they had recently hatched. The incubation period lasted 1 or 2 weeks at most.

In 1971, 1972 and 1973 the distribution of young-of-the-year goldeye was monitored by taking trawl samples in Quatre Fourches, Mamawi Lake, Prairie River and Lake Claire. Samples were collected from June to September in 1972, but only during July in the other years. The sampling data are summarized in Tables 3 and 4. Additional trawl samples were taken in Richardson Lake, Lake Athabasca, Rivière des Rochers, Baril Lake and the Baril River.

From June to July 1972, the number of young-of-the-year goldeve caught by trawling declined drastically throughout the study area (Table 3). For the remainder of the summer. the catch of young goldeve remained relatively constant. The decline in numbers probably reflects a high larval mortality, a common phenomenon for most species of fish.

Throughout the summer of 1972, following the initial decline, the abundance of young

Average number of young-of-the-year goldeye collected from sampling stations at Quatre Fourches, Mamawi Lake, Prairie River and Lake Claire,

	Quati	re Fourches (west)]	Mamawi Lake]	Prairie River	
Sampling dates	$\overline{\mathbf{X}}$	S	N	$\overline{\mathbf{X}}$	S	N	$\overline{\overline{\mathbf{x}}}$	s	N
June 4-16 1972							29.30	57,90	10
June 20-26 1972	18.30	40,20	4	15.70	11.30	9	45.40	26.30	10
July 10-24 1971	0.00	0.00	11	0.20	0.42	10	3.32	12.63	34
July 10-24 1972	9.20	2,23	5	9.20	8.81	10	5,50	5.10	10
July 10-24 1973	2.80	2.79	5	6.10	6.32	10	6,22	6.89	9
Aug. 8-22 1972	5.80	53.44	5	9.00	14.75	10	3.00	4,34	10
Aug. 30-Sept. 14 1972	9.20	16.41	5	5.20	5.93	10	6.00	6.10	10
Sept. 21-27 1972	1.80	1.33	5	2.20	1.60	10	10.33	11,29	9
		Lake Claire north shore)			Lake Claire (west shore)			Lake Claire and east sho	ores)
	\overline{X}	s	N	X	s	N	$\overline{\mathbf{x}}$	S	N
June 4-16 1972	3,77	7.38	13	14.20	14.25	10	3,89	7.65	9
July 10-24 1971	6.25	10.82	4	2.43	2.97	7	0.80	0.98	5
July 10-24 1972	2.00	2.29	16	0.92	2.13	13	1.57	3.27	14
July 10-24 1973	1.37	2.55	15	2.62	2.76	13	0.47	1.31	15
Aug. 8-22 1972	1.35	1.34	14	1.75	3.00	12	0.57	0.90	14
Aug. 30-Sept. 14 1972	******					_ `	0.33	0.47	6

goldeye remained more or less constant in each of the designated areas (Table 3). Areas such as Quatre Fourches (west of the dam), where many larval goldeye were collected, had high densities of young-of-the-year fish throughout the summer. Areas such as Lake Claire (east shore), where few larval goldeye were found, had low densities throughout the summer. This suggests that most young-of-the-year goldeye remain relatively close to the spawning areas, at least until they migrate from the delta.

In 1971 young-of-the-year goldeye were abundant in Lake Claire, but were virtually absent from Mamawi Lake. In all years goldeye were more abundant along the north and west shores of Lake Claire than along the south and east shores. In 1972 the areas of greatest abundance were Mamawi Lake and Quatre Fourches (west of the dam), and in 1973, Prairie River and Mamawi Lake. The differences reflect the areas where goldeye spawned in these years.

In 1971 break-up occurred about 2 weeks earlier than usual. Mature goldeve entered the delta earlier, and were probably well into Prairie River and Lake Claire when water temperatures and other conditions suitable for spawning had developed. In 1972 the dam at Quatre Fourches probably delayed the spawning migration for a few days and provided quiet water conditions west of the dam. Afternoon water temperatures between 20 May and 27 May 1972 were above 12°C for at least 4 days. Kennedy and Sprules (1967) reported that goldeye begin to spawn in quiet waters when temperatures reach 10-13°C. Thus conditions were suitable for spawning west of the dam at Ouatre Fourches and in Mamawi Lake at the time when the inward migration of goldeye was at its peak. These observations indicate that the actual time and place of spawning is dependent on weather, and its effects on break-up and subsequent water temperatures.

Table 4
Distribution of young-of-the-year goldeye in relation to distance from the shore on Lake Claire*

Dist, from shore (m)	No.† samples collected	No. goldeye caught	$\overline{\mathbf{x}}$	s	S²	Samples with no goldeye
10- 150	25	90	3.60	3.12	9.75	0
200- 350	22	30	1.36	1.11	1.23	23
400~ 550	20	13	0.65	0.81	0.67	45
600- 750	14	6	0.43	0.66	0.44	71
800-1000	6	0	0.00	0.00	0.00	100

^{*}X̄, mean no.; S, standard deviation; S², variance.
†The samples were taken at 26 stations, mainly from the sonth, west and north shores of Lake Claire, which had been found in the initial trawl sample (10-150 m from the shoreline) to he productive sites for catching goldeye. Samples were collected July 20-23 and August 15-21 1972 on ealm and usually sunny days.

The variability from year to year in the spawning location is unusual. Ripe goldeye are apparently "areal homing", rather than being "site specific" as are most salmonids.

Table 4 shows the number of young-of-theyear goldeye collected in 87 two-minute trawl samples made at various distances from the shoreline on Lake Claire. All young-of-the-year goldeye were found within 1000 m of the shoreline, over half of these within the first 150 m.

In June 1973, 20 trawl samples were taken in the west end of Lake Athabasca, Rivière des Rochers, Revillon Coupé, the Peace River, and Quatre Fourches (east of the dam). Only six larval goldeye were found in the samples, indicating that these areas were seldom used for spawning. Trawl samples taken in Richardson Lake and Baril Lake indicated that a small population of goldeye spawned in these areas.

When the variance (S^2) in numbers of organisms for a series of samples from a population is larger than the mean (\overline{X}) number, the population is said to have a clumped distribution (MacArthur and Connell 1966). Young-of-the-year goldeye consistently displayed this distribution throughout the study area (Tables 3 and 4). This indicated that the young goldeye formed loose aggregations, although they did not form schools.

In general, trawl samples taken in Chenal des Quatre Fourches showed that young-of-the-year goldeye began to migrate out of the Mamawi-Claire Lake system sometime after mid July, and this migration continued until at least November. There was no consistent peak in this migration in the 3 years in which systematic sampling was carried out. Sprules (1947) reported that young-of-the-year goldeye in the Saskatchewan River Delta were moving into the outlet channels of the spawning lakes early in August, but he did not state when this migration was complete.

4. Year-class strength

Year-class strength can be determined from a selective type of fishing gear by accumulating annual catch data on each year-class from the time it becomes vulnerable to the fishing gear until all individuals of the year-class are dead. Although gill net samples from the adult stock in the delta were taken for only 4 years, these data can be interpreted in a general way. The 1964 and 1965 year-classes (fish which were 6 and 7 years old in 1971) were the dominant fish in samples collected between 1971 and 1974. During these years, they comprised a total of 30 and 25% of the catch, respectively. Both Kennedy and Sprules (1967) and Schultz (1955) have shown that strong year-classes will be well represented in the catch at least until they are 9 and 10 years old. These age groups were never abundant in the early 1970's. This would suggest that the 1961, 1962, and 1963 year-classes were relatively weak. The 1966 to 1968 year-classes (fish which were 6 years old in 1972 to 1974) were also weak. Year-class abundance in the 1970's is probably related to the effects of the 1948 to 1966 commercial fishery.

Survey net samples of goldeye in 1973 showed the 1971 year-class comprised 92.4% of

the immature catch and about 90% of the total population of goldeye which inhabit the delta. Other year-classes of immature goldeye were present, but were poorly represented.

There are probably several factors which could have contributed to the success of the 1971 year-class, but the most important may have been the number of fish spawning in that year. In 1971 a previously successful year-class, that of 1964, entered the spawning population for the first time as mature (7-year-old) fish. It has been previously argued that older year-classes were relatively weak, and consequently the spawning population in 1968, 1969, and 1970 would be small.

Two other factors may have been favourable for young goldeye in 1971. Mature goldeye entered the Mamawi-Claire Lake system about 1 or 2 weeks earlier than in 1972 to 1975, and spawning was completed earlier, resulting in larger young-of-the-year goldeye at the end of the growing season in 1971 than in four other known years. The length of the growing season in this year combined with an abundance of food (Donald and Kooyman 1974) may have contributed to the success of this year-class.

The low water levels which existed throughout the Peace-Athabasca Delta between 1968 and 1971 had no obvious detrimental effect on the goldeye population. The average and minimum water levels in May and the average water level during the summer were similar for all years between 1968 and 1971 (Peace-Athabasca Delta Project Group 1973). It is noteworthy that in 1964 the mean and minimum water levels in May were similar to levels in 1968 to 1971. The 1964 and 1971 year-classes were successful.

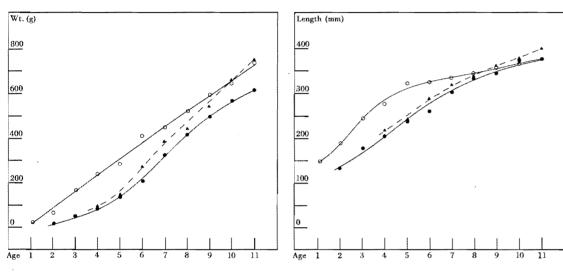
5. Sex ratio of adult goldeye

In 1971, 1972, 1973, and 1974 the adult catch consisted of 24, 18, 17, and 41% adult female goldeye, respectively. The percentage of

Figure 3
The relationship between age and length and weight of goldeye from the Peace-Athabasca Delta in 1947-48 (a) and in 1973 (c), and from the Peace River in 1974 (A). Data for 1947-48 from Kennedy and Sprules (1967)

Figure 3

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females in 1947–48 (Kennedy and Sprules 1967) and in 1954 (Schultz 1955) was 59 and 49%, respectively. The differences between the 1974 and earlier years' catches were related to changes in the age structure of the population, but there is no obvious reason for the discrepancy in the male–female ratio in the early 1970's.

6. Growth rates of adult goldeye

Figure 3 shows the growth rates of goldeye from the Peace-Athabasca Delta in 1947-48 and 1973 and from the upper Peace River in 1974. In 1973 goldeye from the delta were larger than from this same area in 1947-48 and 1954 (Kooyman 1972). Goldeye from the delta in 1971, 1972, and 1974 were similar in size to those in 1973. Consequently, the larger size of goldeye in the early 1970's may be due to a reduction in intraspecific competition for the available food resources during the 1960's and early 1970's,

a factor directly related to the small number of goldeye which were present in the delta.

Goldeye from the upper Peace River differed from those which inhabited the Peace-Athabasca Delta in three ways. First, goldeye from the upper Peace River were distinctly smaller at a given age than those in the Peace-Athabasca Delta (Fig. 3). Second, the age composition in the two areas was quite different. Third, a significant percentage of the mature goldeye in the upper Peace River did not spawn each year (Bishop 1974, and this study), as do the goldeye from Lake Claire and other areas in Canada (Kennedy and Sprules 1967). These characteristics indicate that goldeye in the upper Peace River belong to a distinctly different population from those found in the Peace-Athabasca Delta and lower Peace River.

7. Population dynamics of adult goldeye

The two seasonal migrations of a population of adult fish through the Chenal des Quatre Fourthes provided an opportunity for markrecapture experiments, which furnished data for obtaining estimates of mortality, survival, recruitment, and the size of the population. Adult goldeve were tagged, primarily at Quatre Fourthes in May of 1972, 1973, and 1974 during the spring spawning migration into the Peace-Athabasca Delta. From 1972 to 1975, recovery samples taken during the summer return migration and spring spawning migration of the following year were combined in order to obtain a large recovery catch. The number of goldeye which were tagged (M), and the size of the recovery catch (C) from which recaptured goldeye (R) were obtained are given in Table 5.

Several requirements must be satisfactorily met if estimates of population survival,
recruitment, and size are to be reliable. These
requirements are: (a) marked fish must be randomly distributed throughout the population;
(b) marked fish should not lose their tags;
(c) marked and unmarked fish must have the same
mortality rate; and (d) all fish must be equally
vulnerable to the fishing gear. Donald and
Kooyman (1976) have shown these requirements
were either satisfactorily met or, in the case
of tag loss, could be corrected.

The following population statistics can be estimated by using values for M, C, and R from Table 5, and formulae from Bailey's triple catch method and from the Petersen method (Ricker 1975). We define N₁, N₂, and N₃ as the population size in May 1972, 1973, and 1974, respectively; s₁₂ and s₂₃ as the survival rate from January 1972 to January 1973, and from January 1973 to January 1974; and r₂₃ and r₃₄ as the rate of recruitment from January 1973 to January 1974 and from January 1974 to January

Table 5 Number of goldeye marked, examined and recaptured during four sampling periods						
Time period (t)	Goldeye newly marked	Goldeye examined for marks	Recaptures from 1st marking	Recaptures from 2nd marking	Recaptures from 3rd marking	
May 1972	1375					
$(t_1)'$	(M ₁)					
May 1973	1450	3291	44			
(t2)	(M ₂)	(C2)	(R ₁₂)			
May 1974	1550	3823	53	150		
113	(Ma)	(Ca)	(Real	(B 22)		

(R14)

(R24)

1975 ($r \ge 1$). The values for these population statistics approximately are:

Petersen method

 $N_1 = 100 588$ standard error = $\pm 14 729$

Triple catch method

$N_2 =$	37 231	standard error =	$\pm~8000$
$N_3 =$	18 190	standard error =	± 5175
$s_{12} =$	$0.370\ 13$	standard error =	± 0.05890
$s_{23} =$	0.49537	standard error =	$\pm \ 0.135 \ 83$
$r_{23} =$	0.94677	standard error =	$\pm\ 0.189\ 78$
ro, ==	1 117 93	standard error =	$\pm 0.257.88$

In theory, the rate of recruitment cannot be less than 1. The r_{23} value was less than 1, but nevertheless indicates that recruitment into the adult stock of the population was negligible between 1972 and 1973. This was confirmed by the age structure of the population. In 1972 and 1973, 5- and 6-year-old goldeye were rare. These age classes are the primary source of recruitment into the "catchable" adult population.

The Petersen method provides a reliable estimate of the population size at the time of marking as long as there is negligible recruitment in the time interval between the mark and recapture samples. Therefore, under the prevailing conditions of recruitment in 1972–73,

the population estimate (N_1) calculated by the Petersen method is reliable. This is confirmed when it is compared to an estimate of N_1 obtained by using values from the triple catch method.

 $N_1 = N_2/s_{12}(r_{23})$ = 95.235

Mortality rate estimates can be obtained from catch data by plotting the logarithm of the number of fish at each age against age, and determining the mortality from the resulting "catch curve" (see Ricker 1975). Kennedy and Sprules (1967) found the "catch curve" mortality rate for Lake Claire goldeye in 1947–48 was 42% for fish 8–10 years old. More reliable estimates of mortality rates (1 — s) are obtained from mark-recapture data, and were 63% for 1973–74 and 51% for 1974–75.

The dam at Quatre Fourches provided ideal conditions for a domestic fishery in 1973, but not in 1974 because the dam had washed out. In 1973, we examined 82 domestic catches, obtained 121 tags, and calculated that the domestic fishermen caught 4600 goldeye. The approximate fishing mortality would then be $4600/37\ 231 = 12\%$. Natural mortality would account for 63% - 12% = 51% of the total mortality. This value is identical with the 1974-75 estimate of total mortality which was obtained during a year when the domestic fishing was considerably reduced.

In 1954 the commercial fishery, using 3.75 in. (95 mm) mesh gill nets, produced an estimated 119 000 kg (round weight) of goldeye from the Mamawi-Claire Lake system (Schultz 1955). If the average goldeye in this catch weighed about 450 g (an overestimate), and this fishery removed between 20 and 75% (fishing mortality) of the population, then the goldeye population at this time would have consisted of

between 350 000 and 1 300 000 fish. The estimates of 100 000, 37 000 and 18 000 goldeye for 1972, 1973, and 1974, respectively, clearly indicate that the adult stocks are extremely small even though there has been no commercial fishing since 1966. The adult stocks in this population will probably recover by 1977 or 1978, the years when the 1971 year class will be 6 and 7 years old.

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