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Population Characteristics and Spawning Migration Dynamics of Pink Salmon in U.S. Waters of the St. Marys River

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ABSTRACT. *Population attributes and migratory dynamics of spawning pink salmon* Oncorhynchus gorbuscha *were examined in U.S. waters of the St. Marys River from 1998 through 2002. Spawning migrations were monitored twice each week from late August through early October of each sampling year using a single gill net set immediately below their spawning grounds. Pink salmon were captured between 23 August and 11 October, with the peak migration event in all years occurring between 10 and 22 September. Catch-per-unit-effort was greater in even years (57 fish/night) than in odd years (30 fish/night). Water temperature during spawning migrations ranged from 11.4 to 21.4°C, with nearly 90% of fish captured between 15.0 and 19.7°C. The proportion of females captured (mean = 0.25; range, 0.09 to 0.35) declined after the peak-migration event, with few females caught during October. Total length and wet weight of male and female fish displayed much variability within and among years. Relative condition of male pink salmon declined over the spawning migration, with a sharp decline observed after peak migration events. Pink salmon representing ages 2 through 4 were captured during the study period, with a large percentage (range, 14.6 to 50.6%) of these fish deviating from their usual two-year life cycle. These are the first reported age-3 pink salmon from a Lake Huron tributary and first age-4 fish observed in any freshwater or marine system. Our results suggest that the naturalization of pink salmon to the upper Great Lakes has resulted in system-specific modifications to their potamodromous life history.*

INDEX WORDS: *Pink salmon,* Oncorhynchus gorbuscha*, St. Marys River, spawning migration, population structure.*

INTRODUCTION

Pink salmon *Oncorhynchus gorbuscha* from the Skeena River, British Columbia, were introduced into the Laurentian Great Lakes through the accidental stocking of 21,000 fingerlings into a northern Lake Superior tributary in 1956 (Anas 1959, Schumacher and Eddy 1960, Nunan 1967). This species, which rapidly increased in population abundance and geographic range, had colonized all five Great Lakes by 1979 (Collins 1975, Wagner and Stauffer 1982). Although the abundance and distribution of pink salmon was reported as increasing in Lakes Michigan, Erie, and Ontario during the 1970s and 1980s, only Lakes Superior and Huron currently support notable populations of this species (Emery 1981, Bagdovitz *et al.* 1986, Nicolette and Spangler 1986, Kocik and Taylor 1987, Kelso and Noltie 1990, Kocik *et al.* 1991). Given the proliferation of pink salmon in the Great Lakes over the past four decades, this species has become an important, naturally reproducing component of the Great Lakes fish community.

Pink salmon are native to the Pacific coast of North America where they exhibit a rigid 2-year life cycle that is composed of even- or odd-year stocks of spawning fish (Turner and Bilton 1968, Scott and Crossman 1973, Kwain 1982). Because the initial population of fish in Lake Superior was established from an odd-year spawning stock, it was believed that populations of this species in the Great Lakes would retain their 2-year life cycle and spawn only in odd-numbered years (MacKay 1963, Collins 1975, Wagner 1985). However, Wagner and

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Stauffer (1982) hypothesized that pink salmon in the Great Lakes would exhibit a divergence in spawning periodicity from their parental stock. Although even-year spawning migrations most likely originated from age-3 spawners whose progeny subsequently adopted a 2-year life cycle, there have been several collections of age-3 and precocious age-1 (i.e., jack) pink salmon during both even- and odd-year spawning migrations (Kwain and Chappel 1978, Wagner and Stauffer 1980, Kwain and Kerr 1984, Nicolette 1984, Bagdovitz *et al.* 1986, Nicolette and Spangler 1986). As a result, it would appear that spawning populations of pink salmon in the Great Lakes are comprised of stocks that do not adhere strictly to a 2-year life cycle.

Population attributes and spawning migration dynamics of pink salmon in the Great Lakes have also diverged from their Pacific coast ancestors following their adaptation to a strictly freshwater existence. For example, pink salmon in the Great Lakes are generally smaller in body size than fish of the same age from Pacific coast stocks and spawning migrations are typically comprised of a lower proportion of female spawners (Cooper 1977, Fraser and Fedorenko 1983, Bagdovitz *et al.* 1986, Kwain and Rose 1986, Nicolette and Spangler 1986, Dickerson *et al.* 2002). Further, greater variability in the annual number of spawning fish, timing and duration of the annual spawning migration, gender composition, body size, and age structure of pink salmon populations exists among Great Lakes tributaries (Bagdovitz *et al.* 1986, Kwain and Rose 1986, Nicolette and Spangler 1986, Kelso and Noltie 1990, Noltie 1990, Kocik *et al.* 1991). Because science-based management is dependent upon a basic understanding of these population-level attributes and behaviors, there is a need to improve our knowledge of these life-history features for pink salmon in the Great Lakes.

The objective of this study was to evaluate the population characteristics and spawning migration dynamics of pink salmon in U.S. waters of the St. Marys River from 1998 through 2002. Specifically, we described: (1) total abundance and catch-per-unit-effort for even- and odd-year spawning migrations; (2) the timing of the annual spawning migration and abundance of pink salmon relative to fall water temperature regimes; (3) temporal changes in gender composition; (4) within and among year differences in body size of spawning male and female pink salmon; (5) temporal changes in relative condition of male pink salmon; and (6) the age structure of male and female pink salmon. With this information, we compared the population and spawning migration characteristics of pink salmon in the St. Marys River to those in other tributaries of the upper Great Lakes and Pacific coast of North America.

STUDY SITE

The St. Marys River is a 113-km tributary of northern Lake Huron that originates at Whitefish Bay, Lake Superior. The river flows in a southeasterly direction, with the west and south shores bounded by Michigan and the east and north shores bounded by Ontario. Although the river is relatively short in length, it has a large (21,000 km^2) drainage basin, much of which is covered by Lake Superior which provides 98% of water flow to the river (Duffy *et al.* 1987, Edsall and Gannon 1993). This body of water is a complex, unique ecosystem that is comprised of four distinct lacustrine areas and their respective riverine connecting channels (Fielder and Waybrant 1998). Surface and subsurface currents in the river are highly variable and influenced by discharge from Lake Superior, wind direction, and the passage of commercial vessels (Duffy *et al.* 1987). Hydrologically, the river may be divided into three major reaches: (1) the upper river (22.5 km) extending from Lake Superior to the St. Marys River rapids; (2) the rapids proper (1 km); and (3) the lower river (89 km) extending immediately below the rapids to its confluence with Lake Huron (Duffy *et al.*1987).

The study area for this research was the St. Marys River rapids (herein referred to as the rapids), which are located directly between Sault Sainte Marie, Michigan and Ontario. This reach of the river is approximately 1.2 km in length, 1.6 km in width, and represents 6.1 m of the 6.7 m decline in elevation between Lakes Superior and Huron. This area of the river supports a high discharge (approximately 2,000 m^3/s) and coarse substrates (primarily large cobble and boulders that lie atop underlying bedrock; Duffy *et al.* 1987). However, smaller diameter substrates suitable for lithophilic spawners (e.g., salmonids) are also available. Although, greater than 90% of the total river flow from the rapids has been diverted for the generation of hydroelectric power (Edsall and Gannon 1993), the rapids serve as the primary spawning area for pink salmon, chinook salmon (*O. tshawyscha*), coho salmon (*O. kisutch*), steelhead (*O. mykiss*), Atlantic salmon (*Salmo salar*), and brown trout (*S.

trutta) in U.S. waters of the St. Marys River, as few other suitable spawning areas are present.

METHODS

The annual pink salmon spawning migration in the St. Marys River was monitored from 1998 through 2002. Sampling was initiated between 23 and 25 August and was concluded between 8 and 14 October during each of the 5 study years. For each nightly sampling period, a single monofilament gill net (91.4 m long and 3.7 m deep; 102-mm stretch mesh) was set parallel to the current along the river bottom from a location immediately below the rapids. Sampling took place twice per week during each study year (14 net nights/year), and a gill-net set during each nightly sampling period was for a 4-hr duration from 1900 to 2300 hrs.

All captured pink salmon were measured for total length (TL) to the nearest 1 mm and wet weight to the nearest 1 g. Gender was recorded, and the first four dorsal fin rays were removed for subsequent estimation of age in the laboratory. Gender was determined for each fish based on secondary sexual characteristics. Males were noted by the presence of a kype and an arched (i.e., humped) dorsum, whereas females lacked these characteristics (Scott and Crossman 1973). Further verification of gender was based on the presence of milt (males) and eggs (females), which was determined by exerting light pressure to the abdomen of the fish.

In the laboratory, dorsal fin rays were air dried and subsequently cross sectioned using a rotary tool with a metal cutting blade. Cross sections were examined for each fish at 1.5 to 3.0× magnification using a stereomicroscope following the addition of a drop of 5% acetic acid solution to facilitate differentiation of each annulus. Although only a single reader initially examined each dorsal fin ray cross section, questionable age estimates were analyzed by a second reader. Discrepancies between readers were reconciled with a concert read until agreement was reached.

Although pink salmon eggs hatch and larvae disperse from the spawning sites during winter that same year, there is not an annulus formed during the first wintering period (Nicolette 1984). For example, pink salmon that completed spawning migrations during their second year of life (i.e., 2-year-old fish) displayed only a single annulus. Similarly, pink salmon that displayed two or three annuli were considered to be 3- or 4-year-old fish, respectively.

Annual total catch and catch-per-unit-effort (CPUE; number per gill net night) of pink salmon were examined for each of the 5 study years to detect trends in even- and odd-year spawning migrations. The number of pink salmon captured during each sampling date for a given study year was also examined to identify temporal trends in annual spawning migrations. Due to minor (i.e., 1 to 2 d) differences in sampling dates among years, catch data for each collection date were categorized as standardized, independent sampling units to facilitate subsequent comparisons of temporal trends. For example, the 23 August 1998 and 24 August 1999 collection dates were both assigned to sampling unit 1 of their respective study year. Sampling units 1 through 3, 4 through 11, and 12 through 14 represented pink salmon collections that took place during late August, September, and early October, respectively, for each of the 5 study years.

To examine the timing of annual pink salmon spawning migrations in relation to temporal changes in water temperature, total catch and CPUE data were pooled across the 5 study years for each standardized sampling unit. Daily water temperature data were collected from the Lake Superior State University Aquatic Research Laboratory (Sault Sainte Marie, Michigan), which is located on the St. Marys River approximately 2 km below the rapids. Water temperature recordings for each sampling date were similarly categorized within each respective 1°C thermal unit (i.e., 11.0 to 11.9°C were assigned 11°C, etc.).

Total length and wet weight data from male pink salmon were pooled for all 5 study years and used to calculate relative condition (K_n) as:

$$K_n = W/W',$$

where W was the measured wet weight and W' was the length-specific expected wet weight as predicted by a weight-length regression equation developed for that population (LeCren 1951). Female pink salmon that were captured during spawning migrations were not included in this analysis due to small sample sizes for each spawning period. To examine temporal trends in body condition of male pink salmon, each annual spawning migration was divided into five periods, with each period containing three sampling units except period three which contained only two sampling units.

Age-specific comparisons of median total length and wet weight of pink salmon were made for fish captured during the 2000 through 2002 sampling years. Age- and gender-specific data for the 1998 and 1999 sampling years were not available, so these years were not included in our analyses. Total length and wet weight were compared between genders within a sampling year using a Mann-Whitey U-test, and for each gender among years using a Kruskal-Wallis one-way analysis-of-variance (ANOVA) on ranks using a chi-square approximation. When a significant difference was detected among years, a Dunn's multiple comparisons procedure was used to separate the medians.

Median relative condition of male pink salmon was compared among five spawning migration periods using a Kruskal-Wallis one-way ANOVA using a chi-square approximation. When a significant difference was detected, a Dunn's multiple comparisons procedure was used to separate the medians. The number of male and female pink salmon and proportion of female fish captured during each sampling unit for all 5 study years were examined to determine temporal changes in gender composition. Age frequency for male and female pink salmon was determined for each study year, and the percentage of the annual catch represented by each cohort was reported for each gender. The age frequency of male and female fish were summed to express the total age frequency and percent composition of each cohort for pink salmon captured during each sampling year. Methods of statistical testing followed those as outlined in Zar (1999), and all statistical analyses were conducted at an α = 0.05 level of significance.

RESULTS

The total catch of pink salmon in the St. Marys River diverged between even and odd sampling years (Fig. 1). The number of spawners captured was greatest during even years, with 627 and 601 fish collected in 1998 and 2000, respectively. Although the pink salmon catch in 2002 also followed this pattern, the number of fish captured in this year (N = 1,181) was greater than the other even years by more than 550 individuals. Fewer spawners were captured during odd years, with 381 and 454 fish captured in 1999 and 2001, respectively. Trends in catch-per-unit-effort were similar to patterns in total catch data, with CPUE greater during even sampling years (57 fish/night) than in odd sampling years (30 fish/night).

The number of pink salmon captured during each sampling year exhibited a unimodal distribution (Fig. 2). Pink salmon were always captured in the first gill-net set and all subsequent sampling dates through 11 October of each study year. The number of pink salmon captured during each standardized sampling unit increased until a peak migration event, which occurred between sampling units 6 and 9 (10 through 22 September). During even sampling years, greater than 110 fish (range, 113 to 201) were captured during the peak spawning migration. In contrast, fewer than 100 fish (range, 75 to 76) were captured during odd sampling years.

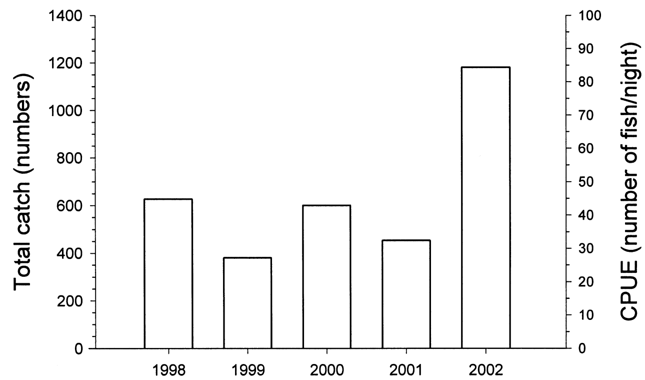

FIG. 1. Total catch and catch-per-unit-effort (CPUE) of pink salmon captured during annual spawning migrations in U.S. waters of the St. Marys River, 1998–2002. Bars relate equally to each Y-axis because effort was equal among years (14 net nights).

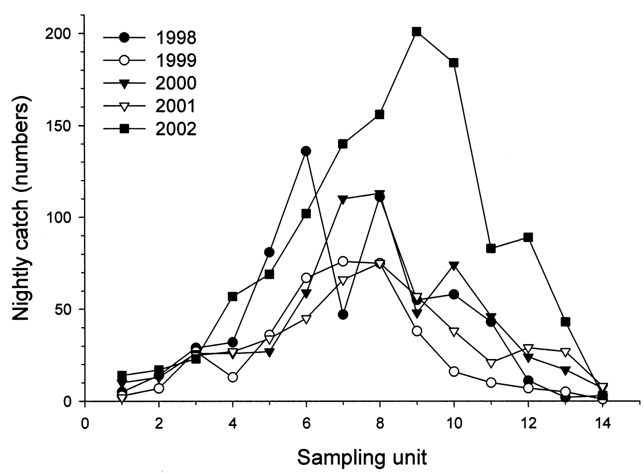

FIG. 2. Number of pink salmon captured during each standardized sampling unit of the 1998–2002 annual spawning migrations in U.S. waters of the St. Marys River. For definitions of each sampling unit, see the Methods section.

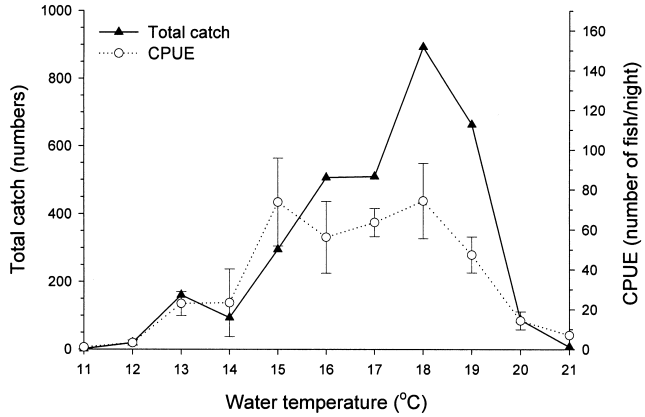

FIG. 3. Pooled total catch and catch-per-unit-effort (CPUE) of pink salmon captured during the 1998–2002 annual spawning migrations in U.S. waters of the St. Marys River versus categorical water temperature data. Error bars for CPUE data represent ± 1 SE.

The number of pink salmon captured immediately following the peak migration declined sharply and approached zero by the end of each sampling year.

Pink salmon were caught between 23 August and 11 October at water temperatures that ranged from 21.4 to 11.4°C (Fig. 3). Approximately three-fourths (72%) of all pink salmon were captured between 15.0 and 18.9°C, with 88% of fish captured between 15.0 and 19.7°C. The first peak in the spawning migration occurred between 17.2 and 18.5°C, with the exception of 2000 when the first peak occurred at 15.2°C. Only 3% of the total catch occurred at temperatures above 19.7°C and less than 1% of fish were captured below 13.0°C. Catch-per-unit-effort followed the same general trend, with the highest CPUE values observed between 15.0 and 19.7°C.

Body size of pink salmon differed between male and female fish during annual spawning migrations (Table 1). Although the median total length of age-2 male pink salmon was significantly greater than age-2 female fish in 2000, 2001, and 2002, there were no significant differences in wet weight during these years (Table 2). Age-3 male fish were significantly longer and heavier than age-3 females in 2000 (male N = 33; female N = 16, length: $U = 224.5$; $P < 0.01$ and weight: $U = 277.0$; $P < 0.01$), while there were no significant differences in total length or wet weight between genders in 2001. Although, age-3 male pink salmon were greater in total length in 2002 (male N = 52; female N = 23; $U = 638.5$; $P < 0.01$), wet weights of male and female pink salmon were not significantly different ($U = 884.5$; $P = 0.91$).

TABLE 1. Median total lengths and wet weights of male (M) and female (F) pink salmon captured during annual spawning migrations in U.S. waters of St. Marys River, 1998–2002. Values in parentheses represent 1 standard deviation. Lengths and weights without a standard deviation are due to a sample size of one.

Year	Gender	Age	Total length (mm)	Wet weight (g)
2000	M	2	470 (23)	856 (155)
	F		450 (15)	866 (86)
	M	3	487 (32)	977 (228)
	F		446 (18)	850 (65)
	M	4	459	837
	F		492	946
2001	M	2	439 (26)	698 (124)
	F		423 (16)	745 (77)
	M	3	446 (26)	721 (191)
	F		445 (17)	815 (149)
	M	4	472 (22)	976 (202)
	F		448	824
2002	M	2	452 (23)	794 (141)
	F		446 (21)	836 (151)
	M	3	472 (29)	933 (166)
	F		456 (19)	895 (124)
	M	4	476 (17)	1000 (150)
	F		446 (16)	807 (37)

Total length and wet weight of male and female fish varied significantly among years. The median total length and wet weight of males ages 2 and 3 varied significantly among years (length: both $df = 2$; $H = 50.94$ and 15.24, respectively; both $P < 0.001$ and weight: both $df = 2$; $H = 43.67$ and 21.29, respectively; both $P < 0.001$), with age-3 males

TABLE 2. Sample sizes, test statistics, and P-values for Mann-Whitney rank sum tests comparing pink salmon total length and wet weight between genders within each sampling year from 2000 to 2002.

Year	Gender M	Gender F	Total length *U*	Total length *P*	Wet weight *U*	Wet weight *P*
2000	126	56	3,401	< 0.01	5,151	0.94
2001	75	13	339	< 0.01	670	0.29
2002	51	33	1,175.5	0.04	1,591	0.08

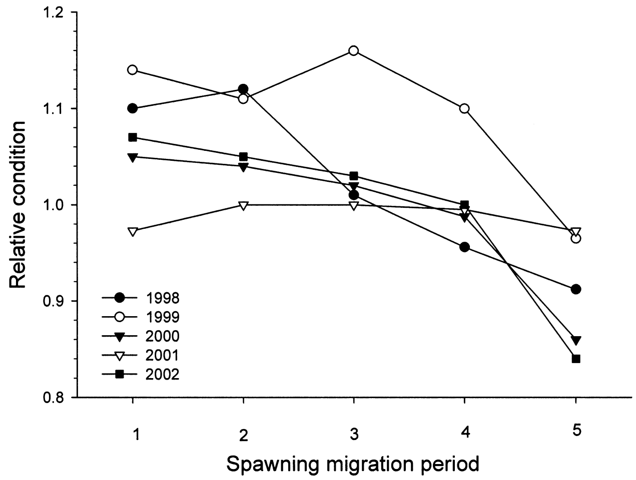

FIG. 4. Relative condition of male pink salmon captured during each annual spawning migration from 1998–2002 in U.S. waters of the St. Marys River. For the definition of each period during spawning migrations, see the Methods section. Female pink salmon that were captured during spawning migrations were not included in these analyses due to small sample sizes.

TABLE 3. Dunn's multiple comparisons test statistics (**Q**) *for within-year comparisons of relative condition for pink salmon captured during annual spawning migrations in U.S. waters of the St. Marys River, 1998–2002. There are no comparisons for the 2001 sampling year because there were no significant differences in relative condition among spawning periods. Values with an asterisk represent a statistically significant difference* (**P** *< 0.05)*

Spawning period	1998	1999	2000	2002
1 vs 2	1.27	1.78	0.18	0.02
1 vs 3	2.18	0.25	1.73	1.54
1 vs 4	4.27*	2.67	3.85*	3.77*
1 vs 5	3.82*	4.72*	7.04*	9.26*
2 vs 3	4.55*	3.09*	2.61	2.54
2 vs 4	8.01*	1.38	5.38*	6.67*
2 vs 5	5.01*	4.05*	8.46*	13.67*
3 vs 4	2.43	4.00*	3.46*	4.24*
3 vs 5	2.63	5.42*	7.27*	12.14*
4 vs 5	1.48	3.19*	4.91*	9.69*

being longer and heavier. Total length and wet weight of age-2 males were significantly different between each year with the exception of wet weight in 2000 and 2002 (length: $Q = 1.60$; $P > 0.05$ and weight: $Q = 1.64$; $P > 0.05$). While total length and wet weight of age-2 female fish were significantly different among sampling years (length: $df = 2$; $H = 24.05$; $P < 0.001$ and weight: $df = 2$; $H = 18.91$; $P < 0.001$), there were no significant differences between total length and wet weights of age-3 female fish (length: $df = 2$; $H = 1.69$; $P = 0.43$ and weight: $df = 2$; $H = 5.49$; $P = 0.06$). Trends in total length and wet weight differences among years were not detected for either gender.

Body condition of male pink salmon declined over the spawning migration period (Fig. 4). Relative condition of male pink salmon was significantly different among the five spawning migration periods in all years (1998 [$H = 80.26$; $P < 0.01$]; 1999 [$H = 43.03$; $P < 0.01$]; 2000 [$H = 91.48$; $P < 0.01$]; 2002 [$H = 220.40$; $P < 0.01$]), with the exception of 2001 ($H = 3.96$; $P < 0.01$; Table 3). Male pink salmon captured during period five had significantly lower median relative condition than males captured during periods one, two, and three (i.e., through peak migration) in all sampling years, with the exception of 1998. Similarly, fish captured during period three had significantly higher relative condition than fish captured during periods four and five (i.e., peak migration and post-peak migration, respectively) in all sampling years, with the exception of 1998.

The pink salmon catch became increasingly dominated by male fish over the spawning migration during each sampling year (Fig. 5). Males com-

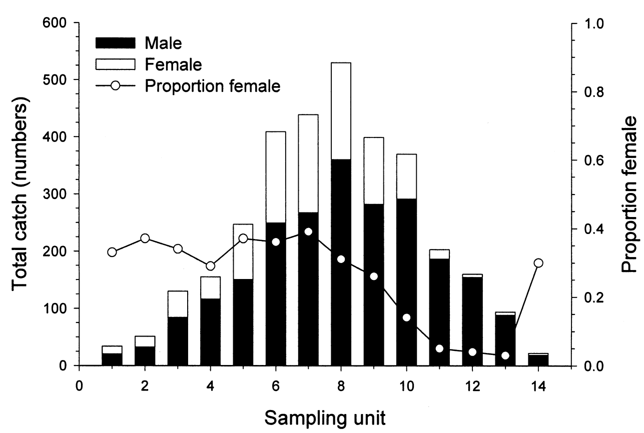

FIG. 5. Pooled number of male and female pink salmon and proportion of female pink salmon captured during each standardized sampling unit of the 1998–2002 annual spawning migrations in U.S. waters of the St. Marys River. For definitions of each sampling unit, see the Methods section.

TABLE 4. Frequency of male (M) and female (F) pink salmon captured in each age category during annual spawning migrations in U.S. waters of the St. Marys River, 1998–2002. Values in parentheses for each age category represent percentage data.

		Age (years)		
Year	Gender	2	3	4
1998	M	336 (88.0)	46 (12.0)	
	F	60 (73.2)	21 (25.6)	1 (1.2)
	Total	396 (85.4)	67 (14.4)	1 (0.2)
1999	M	44 (63.8)	25 (36.2)	
	F	19 (38.0)	31 (62.0)	
	Total	63 (52.9)	56 (47.1)	
2000	M	119 (77.8)	32 (20.9)	2 (1.3)
	F	55 (79.7)	14 (20.3)	
	Total	174 (78.4)	46 (20.7)	2 (0.9)
2001	M	75 (62.5)	41 (34.2)	4 (3.3)
	F	13 (50.0)	12 (46.2)	1 (3.8)
	Total	88 (60.3)	53 (36.3)	5 (3.4)
2002	M	51 (46.4)	53 (48.2)	6 (5.4)
	F	33 (55.0)	24 (40.0)	3 (5.0)
	Total	84 (49.4)	77 (45.3)	9 (5.3)

prised the largest proportion (mean = 0.75; range, 0.65 to 0.91) of the annual pink salmon catch in each year. The mean proportion of females captured during each sampling unit remained near 0.35 through the peak spawning migration, but decreased rapidly following the peak migration. Observed values for the proportion of females in the annual (total) catch ranged from 0.09 in 2001 to 0.35 in 1999 (mean = 0.25).

Pink salmon representing ages two through four were captured during the five-year study period, with a substantial percentage (14.6 to 50.6%) of fish captured in each sampling year greater than age two (Table 4). Two- and 3-year-old pink salmon were represented in the annual catch for each sampling year (range, 49.4 to 85.4% and 14.4 to 47.1%, respectively). In addition, 4-year-old pink salmon were captured in all years with the exception of 1999 (range, 0.2 to 4.7%). Both male and female pink salmon were present in all age classes of fish captured.

DISCUSSION

Since their introduction into the Laurentian Great Lakes, spawning migrations of pink salmon have predominantly occurred during odd years (Wagner and Stauffer 1982, Nicolette and Spangler 1986, Kocik *et al.* 1991). Even-year spawning migrations were first observed in Lake Huron in 1976, but were uncommon through the late 1980s and consisted of a low numbers (i.e., 1 to 7 fish) of spawners (Kocik *et al.* 1991). Wagner and Stauffer (1982) predicted that the presence of 3-year-old spawners would reduce the differences in spawner abundance in the Great Lakes between odd-and even-year spawning migrations. Although variability exists in the number of spawners among years, there has been a shift in dominance from odd- to even-year spawning migrations in the St. Marys River. This shift is not unique to Lake Huron, as a similar occurrence was noted in Lake Superior by Bagdovitz *et al.* (1986).

According to Noltie (1990) and Kocik *et al.* (1991), pink salmon spawning migrations in Lake Superior occur during the same time of the year as Pacific coast stocks (i.e., late August through early October). In the St. Marys River, spawning migrations of pink salmon also occurred during this time period. Based on catch data, spawning migrations of pink salmon in the St. Marys River peaked in mid-September, which was within the range of observed peak spawning migrations reported for tributaries of Lake Superior (Kwain and Rose 1986, Nicolette and Spangler 1986, Kelso and Noltie 1990, Noltie 1990). However, peak migration in the St. Marys River in 2002 was observed at a later date (22 September) than any of the other sampling years. This delay in the timing of the peak spawning migration may have resulted from a much greater number of spawners that year which is similar to observations for many Pacific coast tributaries (Groot and Margolis 1991). The decline in catch following the peak migration may be attributed to the large number of fish that had already entered the rapids to spawn. The slight increase in catches two to four sampling units following the peak migration, observed in all sampling years with the exception of 1999, was likely due to male fish that had completed spawning activities and were exiting the rapids. Further, the low relative condition values for male pink salmon captured during the fourth and fifth spawning migration periods support this presumption. The temporal uniformity associated with initial capture, peak migration, and last capture of pink salmon suggests that migration dynamics of this species are strongly influenced by photoperiod.

Spawning migrations of pink salmon in the St. Marys River occurred at water temperatures that were greater than those observed for Lake Superior tributaries. Water temperature at the time of first capture in our study was greater than those observed in tributaries of Lake Superior (Kwain and Rose 1986, Nicolette and Spangler 1986, Noltie 1990). Kwain and Rose (1986) reported that most pink salmon in the Carp and Pancake rivers were captured at water temperatures that ranged from 10 to 17°C. In contrast, the majority of pink salmon in the St. Marys River during our study were captured between 15 and 19.7°C. Nicolette and Spangler (1986) reported peak spawning migrations for pink salmon at water temperatures that ranged from 8.9 to 14.4°C in the Cascade and Cross rivers. All peak spawning migrations in the St. Marys River occurred at greater water temperatures (approximately 4°C warmer) and fell within a narrower range (i.e., 15.2 to 18.5°C) than those observed for Lake Superior tributaries. The last pink salmon captured during each sampling year in the St. Marys River also occurred at greater water temperatures (i.e., 11.4 to 13.7°C) than the 4.0 to 9.5°C reported for Lake Superior (Kwain and Rose 1986, Noltie 1990). The difference in water temperatures between Lake Superior tributaries and the St. Marys River is most likely due to the high heat budget of Lake Superior which provides 98% of water flow to the St. Marys River. Tributaries of Lake Superior have much lower heat budgets and, as a result, cool at a much greater rate. If spawning at warmer temperatures is driven by the temporal uniformity of annual migrations in both lakes, then photoperiod may be a more dominant releasing stimulus for pink salmon spawning migrations than water temperature. Onshore winds, heavy precipitation events, and changes in water temperature have also been hypothesized as potential releasing stimuli that initiate pink salmon spawning migrations, but their importance and interactions are not well understood (Kwain and Rose 1986, Kelso and Noltie 1990, Noltie 1990).

The observation that male pink salmon in the St. Marys River were significantly greater in total length than females within each sampling year was similar to previous reports for fish in Lake Huron and Pacific coast tributaries (Beacham and Murray 1985, Kocik *et al.* 1991). However, differences in total length between genders within a given year have been inconsistent in Lake Superior (Nicolette and Spangler 1986, Noltie 1990, Kocik *et al.* 1991). For example, male pink salmon captured in Lake Superior tributaries by Noltie (1990) and Kocik *et al.* (1991) were significantly greater in length than female fish, while Nicolette and Spangler (1986) reported no difference in total length between genders. During years when male fish in Lakes Superior and Huron were longer than females, they were also heavier (Noltie 1990, Kocik *et al.* 1991). Our results differ from these studies because male pink salmon from the St. Marys River were greater in total length, although fish wet weight between genders within a sampling year was not different with the exception of 2000. Although male and female pink salmon in the St. Marys River varied in total length and wet weight among years, no trends were detected. This among-year variability may be attributed to density-dependent mechanisms related to pink salmon abundance or forage availability as have been hypothesized for other Great Lakes stocks of this species (Nicolette and Spangler 1986, Kocik *et al.* 1991).

Few differences in relative condition of male pink salmon in the St. Marys River were observed among the first three spawning migration periods. These fish most likely were in similar condition because they were "fresh" fish that had not yet undergone spawning activities. However, there were significant differences detected between fish captured during spawning periods one through three relative to periods four and five in all years except 1998. These results indicate that fish captured during periods four and five were likely "dropback" males that had already completed reproductive activities and were exiting the rapids. The rapid decline in relative condition between spawning migration periods three and four may be due to a difference in the movement patterns of fish captured during these periods. For example, pink salmon that were captured during period three were comprised primarily of fresh fish still migrating upriver to their spawning grounds. In contrast, the majority of fish captured during periods four and five appeared to be dropback fish that were leaving the rapids and returning downstream. Fresh fish captured prior to spawning periods four and five probably had higher relative condition values than those captured during periods four and five because they had not yet undergone spawning activities (e.g., redd construction, territorial behaviors, gamete extrusion, etc.) that would result in the loss of body mass and lower relative condition values.

The proportion of female pink salmon in the annual spawning migration for the St. Marys River was highly variable among sampling years. However, the proportion of females in this system was consistently lower than those observed in tributaries of Lake Superior and for Pacific coast stocks (Kwain and Rose 1986, Nicolette and Spangler

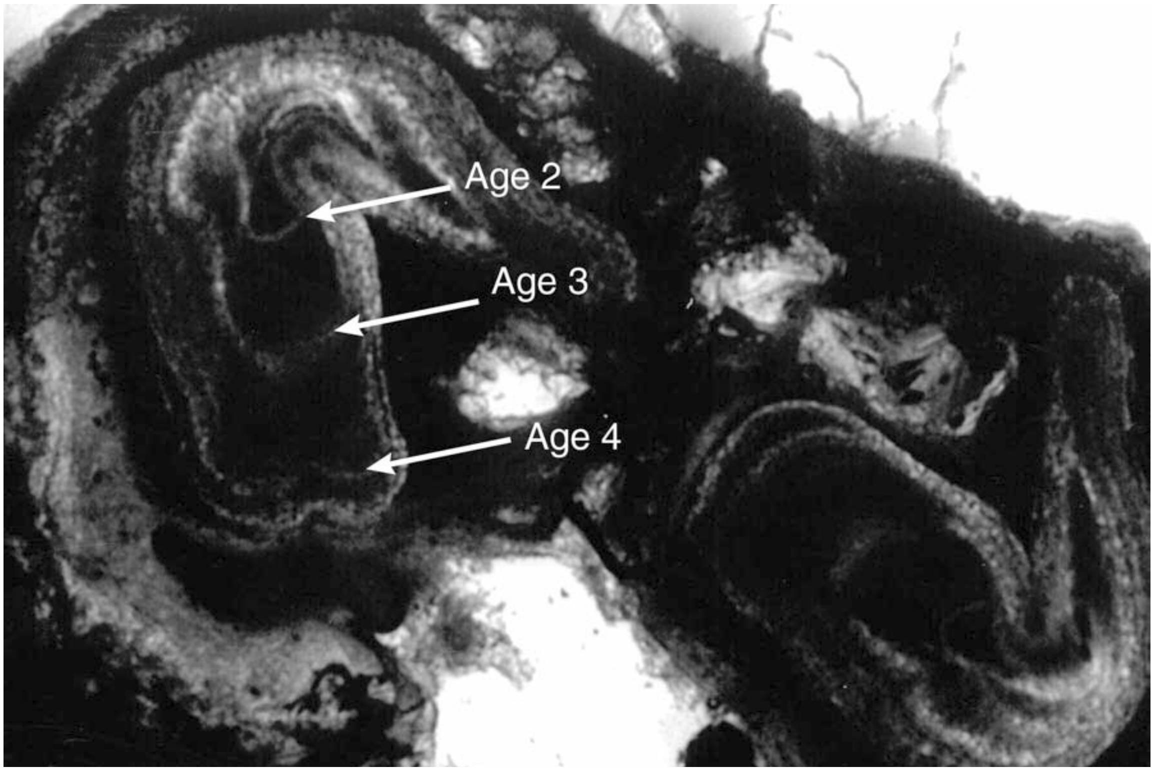

FIG 6. Fin ray cross-section (2X) of an age-4 pink salmon captured during the 2002 spawning migration in U.S. waters of the St. Marys River.

1986). Spawning migrations of pink salmon in Lake Superior tributaries either increased in the proportion of females over the spawning migration or remained constant (Kwain and Rose 1986, Nicolette and Spangler 1986, Noltie 1990). In contrast, females in the St. Marys River comprised a relatively constant proportion of the catch during the first half of the spawning migration (i.e., until mid-September), after which time it decreased rapidly. Male dominance was most apparent in October, during which time only seven female fish were captured. Despite the low number (i.e., small proportion) of female spawners, the St. Marys River population of pink salmon is entirely self-sustaining and there was no apparent decline in pink salmon abundance during our study period.

The decline in the proportion of female fish captured over the course of each spawning migration may be attributed to higher energetic demands on female pink salmon during this time. Idler and Clemens (1959) reported that sockeye salmon in the Fraser River used 91 to 96% of their lipid stores during spawning migrations. However, male sockeye salmon used 30% of carcass protein stores, stored in muscle and structural tissue, while female fish used 41% of these reserves (Idler and Clemens 1959, Diana 1995). The decrease in the proportion of female pink salmon in the St. Marys River captured after the peak spawning migration may be a result of female fish succumbing more rapidly after spawning due to loss of body mass. As a result, these fish, having lost a large amount of muscle tissue, would be unable to exit the rapids and be captured in our net. In contrast, males would have used fewer energy stores and retained enough functional muscle mass to actively move downstream and be captured in the gill net.

The age structure of pink salmon in the St. Marys River was comprised of a larger proportion of fish that deviated from the typical two-year life cycle than has been previously reported for other Great Lakes tributaries (Kwain and Kerr 1984, Nicolette 1984, Bagdovitz *et al.* 1986, Nicolette and Spangler 1986, Kocik *et al.* 1991). While 3-year-old fish have been documented in a number of tributaries of Lake Superior, this study is the first to report an age-3 pink salmon in a Lake Huron tributary (Wagner and Stauffer 1980, Kwain 1982). Our study results also include the first report of a 4-year-old pink salmon in any freshwater or marine system (Fig. 6). In Lake

Superior, pink salmon that exhibited delayed sexual maturity and were older at the time of spawning were thought to have resulted from lower growth rates in this oligotrophic environment (Kwain and Chappel 1978, Wagner and Stauffer 1980). Kocik *et al.* (1991) reported no differences in body size of pink salmon between Lakes Superior and Huron. This similarity in body size may be attributed to comparable environmental conditions experienced by pink salmon between these lakes, thereby resulting in similar growth patterns and consequently delayed sexual maturity for these systems. Although this is the first report of an age-4 pink salmon in the wild, Kwain (1982) reported that pink salmon reached sexual maturity at ages 2 through 4 in a freshwater laboratory environment. Our study indicates that variability in age-at-sexual maturity for Great Lakes stocks of pink salmon is no longer unique to Lake Superior, and the proportion of fish exhibiting delayed sexual maturity appears to have increased from historical levels.

Our results suggest that the naturalization of pink salmon in the upper Great Lakes has resulted in system-specific modifications to their potamodromous life history. Variability observed in population characteristics and migratory dynamics within and among years appears to have been influenced by both biotic and abiotic factors. However, these factors and their relationships are not well understood and should be examined in future studies. As a result, the development of science-based management programs for pink salmon will require continued study of both even and odd-year stocks of this species throughout their range in the Great Lakes.

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