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ARTICLE

A Comparison of Age, Size, and Fecundity of Harvested and Reference White Sucker Populations

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Abstract

White Suckers *Catostomus commersonii* are an important source of fresh bait for the Maine lobster fishery. The Maine Department of Inland Fisheries and Wildlife began issuing commercial harvest permits in 1991, without reporting requirements or limits on the number of permits. There is recent concern that overfishing may be occurring. To infer impact, we investigated demographic differences between White Sucker populations in lakes open to harvest and those in lakes closed to harvest. Each of three harvested lakes was paired to a nearby closed lake as a reference based on general size, morphometry, and information on harvest pressure. In total, 976 spawning White Suckers were collected from the six lakes in 2014 (120–282 individuals/lake). Fish size, estimated age, fecundity, and mortality rates were compared between lakes. We hypothesized that we would find smaller, younger, and less-fecund individuals in harvested lakes compared to reference lakes. Size and age distributions for both sexes differed between nearly all lake pairs (except between males from one pair). White Suckers from reference lakes were larger and older and had greater gonadosomatic indices and fecundity than fish from harvested lakes. Estimated annual mortality rates were at least twofold higher in harvested lakes than in reference lakes. We detected some differences in von Bertalanffy growth parameters between lake pairs, as might occur under selective harvest pressure. The growth coefficient was smaller for reference lakes than for harvested lakes, while asymptotic length was greater for reference lakes than for harvested lakes. The data suggest that current levels of exploitation are resulting in greater age truncation in existing White Sucker populations.

Overharvesting may result in changes in life history traits for many long-lived and short-lived fish species. The degree and duration of harvesting can result in a combination of phenotypic (i.e., expressed traits) and genotypic (i.e., evolutionary) changes in trait means that ultimately dictate the probability of population persistence (Brown et al. 2008; Sharpe and Hendry 2009; Durant et al. 2013). A trait distribution is the product of the genetic (evolution), environmental (phenotypic plasticity), and demographic (e.g., selective mortality, immigration, emigration, births, growth, etc.) processes operating on a population at a given time (Pelletier et al. 2009; Sharpe and Hendry 2009; Reed et al. 2010). With the direct demographic effects of selection through harvest, mean trait changes are often plastic in nature. However, prolonged and intense harvest pressure can induce an evolutionary shift (i.e., change in growth, age truncation, reduced fecundity, and accelerated maturity) that may persist for many generations (Jørgensen et al. 2007; Brown et al. 2008; Enberg et al. 2012). Chronic size-selective pressure removes fish with traits that are desirable to humans (e.g., larger size and faster growth) and favors undesirable traits, which may persist after selection has ceased (Anderson et al. 2008; Conover et al. 2009; Durant et al. 2013). Such shifts have been documented in many commercial fishery stocks over the past 20 years, but directly linking harvest with

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these changes remains challenging (Jørgensen et al. 2007; Conover et al. 2009; Sharpe and Hendry 2009).

The size-selective harvest of larger, faster-growing individuals can result in populations that are dominated by slow-growing individuals (Conover and Munch 2002; Hamilton et al. 2007), yet these changes in growth are difficult to monitor due to the complex interaction of individual and population behaviors, morphology, and physiology (Enberg et al. 2012). These traits couple with extrinsic (e.g., harvest and environmental conditions) and intrinsic (e.g., density dependence, competition, and predation) factors to further complicate the expression of growth rates within a population (Conover et al. 2009). In addition to the concern that size-selective harvest removes individuals with a genetic predisposition toward fast growth, the removal of large fish often targets older individuals, with age truncation as the more immediate result.

Managers are concerned that the direct effect of removal through unregulated or excessive harvesting may compromise a population's viability and have indirect effects on important traits, such as reproductive potential. The number of eggs that an individual female can produce and carry correlates to body size: the larger the female, the greater the fecundity (Koslow et al. 1995; Conover et al. 2009; Brunel 2010). If a population is dominated by smaller individuals, the total number of eggs produced will be lower than that produced by a population not subject to harvest. Such a change may alter the population's viability (Winemiller 2005). This has been explored in the overharvested Atlantic Cod *Gadus morhua* fishery in North America, and some researchers doubt whether Atlantic Cod populations will rebound in the near term (Trippel 1995). Fishing mortality coupled with natural mortality may create a risk of population collapse if the removal of individuals—especially large, fecund females—is rapid (Brown et al. 2008).

A decrease in age at maturity is another indirect effect of harvest-mediated trait changes that could lower a population's viability (Trippel 1995; Brunel 2010). Under harvest regimes that are selective for large-sized fish, early maturation is selectively favored because it increases the fish's opportunity to spawn prior to harvest. Older fish, however, have the competitive advantage of greater fat stores, which provide energy for overwintering and postspawn survival (Berkeley et al. 2004). Alternatively, diminished fecundity and a lack of energy stores contribute to recruitment variability and reproductive failure (Berkeley et al. 2004; Anderson et al. 2008). Trippel (1995) investigated temporal demographic changes in Atlantic Cod and other commercially important ocean fish species in response to stock decline, and they found that age at maturity decreased as the population size decreased. This also was correlated with a decrease in mean population size and fecundity. For longer-lived species, it is unclear whether trait trends reflect fishery-induced evolution or simply environmentally mediated demographic processes.

For this study, we investigated demographic differences in long-lived White Sucker *Catostomus commersonii* populations, which may also be experiencing trait changes from fishery-induced evolution and environmentally mediated processes. The White Sucker is an important species found in a variety of habitats ranging from streams and rivers to ponds and lakes (Thompson and Beckman 1995; Wakefield and Beckman 2005; McManamay et al. 2012). During their spawning season in spring, they migrate en masse up tributaries, where they directly (e.g., feces and gametes) and indirectly (e.g., bioturbation) provide energy and nutrient subsidies that fuel headwater production and support desirable sport fish (Vanni 2002; Sanderson et al. 2009; Childress et al. 2014). Nutrients and energy that are translocated from adult habitats to spawning habitats play an essential ecological role in freshwater systems.

Historically, White Sucker juveniles were harvested predominantly as bait for recreational fishing in the State of Maine; later, a commercial fishery for adults to be used as bait for American lobsters *Homarus americanus* developed in 1991 (Michael Brown, Maine Department of Inland Fisheries and Wildlife [MDIFW], personal communication). Maine allows the harvest of reproductive individuals (including prespawn adults) during the spawning season (April–June) in all but a few waterbodies. An unlimited number of permits is issued each year, and harvesters have not been required to report their White Sucker landings. As a result, harvest of White Suckers in Maine is poorly characterized. The MDIFW has closed several waterbodies to mitigate the potential impacts of commercial harvest. These concerns are driven in part by the White Suckers' presumed role as prey for the highly valued Lake Trout *Salvelinus namaycush* (Chen and Harvey 1999; Smith et al. 2008; Merry Gallagher, MDIFW, personal communication).

Our goal was to investigate the influence of harvest pressure on White Suckers in Maine lakes by using a weight-of-evidence approach. This study represents an important first look at life history traits for White Suckers harvested in Maine waters. To compare population demographics, White Suckers were collected from lakes that were open and closed to commercial harvest. We addressed two main objectives: (1) to determine the age structure and size structure of White Suckers in lakes that were closed and open to harvest; and (2) to infer the effects of harvest on White Sucker fecundity. We hypothesized that harvested populations would have narrower size distributions and younger age structures than populations that were protected from harvest. This was expected to be associated with lower total fecundity due to the dominance of younger, smaller individuals in the harvested populations.

METHODS

Study sites.—In 2014, we sampled six lakes during April–June, when White Sucker commercial harvest is open in Maine.

Three of the lakes were subject to commercial harvest (hereafter, "harvested lakes"), whereas the remaining three were considered effectively closed to harvest (hereafter, "closed [reference] lakes"). The three harvested lakes were Graham Lake (44°35′N, 68°23′W), Unity Pond (44°36′N, 69°20′W), and Millinocket Lake (45°40′N, 68°42′W). The MDIFW identified these locations as being popular for commercial harvesters based on the number of permits issued since 1991; the popularity of the three lakes is likely attributable to their easy accessibility from the road (most harvesters select their harvesting locations this way).

Due to the sparse and incomplete data set on White Sucker harvest in the state, we were unable to choose our study lakes at random. Each harvested lake was paired with a closed reference lake based on general size, geography, depth, and general fish community characteristics (pairs A, B, and C; Table 1) as informed by regional MDIFW biologists. Reference lakes were Pushaw Lake (44°59′N, 68°51′W; paired with Graham Lake), Chemo Pond (44°49′N, 69°33′W; paired with Unity Pond), and Cold Stream Pond (44°14′N, 68°33′W; paired with Millinocket Lake; Figure 1). Pushaw Lake and Cold Stream Pond had been closed to harvest since 2010. Chemo Pond was open to White Sucker harvest but was assumed to host little pressure due to its remote location and minimal listing through permitting (only one recent permit had been issued in 2009). All sample lakes except Pushaw Lake were also open for baitfish collection (which may include juvenile White Suckers for sport fishing) during the year, but the level of harvest for baitfish was unknown.

Fish collection.—After ice melt, we collaborated with three experienced harvesters who used their own gear and opportunistically sampled White Suckers by using several gear types: trap net (mesh size = 0.75 cm^2); rigid, single-door, XL-fish trap with extension wings (Tomahawk LiveTrap, Hazelhurst, Wisconsin; mesh size = 1 × 1 in, 14 gauge); modified lobster pot (mesh size = 1 × 1 in, 14 gauge); hoop net (mesh size = 1 cm^2); and hand-made trap (mesh size = 1 cm^2). Traps were set upstream and were left overnight to target spawning individuals (Table 2 provides details on the locations and lake-specific efforts). Lakes were harvested sequentially as water temperature increased above 10°C, coincident with the beginning of the spawning run (Geen et al. 1966). White Suckers were euthanized through cervical transection (according to Institutional Animal Care and Use Committee protocol) and were processed on the day of capture. In the laboratory, we recorded biological data, including FL, total mass, and sex, for each individual. We then removed gonads and heads for use in fecundity and age analyses.

Age and growth estimation.—Left and right lapilli (the largest otoliths in White Suckers; Sylvester and Berry 2006) were removed from each fish. Otoliths were set in epoxy resin and were then sectioned along the transverse plane. The section was mounted on a slide with clear Crystalbond 509 (SPI Supplies and Structure Probe, Inc., West Chester, Pennsylvania) and was wet sanded until annuli could be distinguished (Sylvester and Berry 2006). Sanded otoliths were placed under a dissecting scope (40×) and photographed with SPOT version 5.1 (SPOT Imaging, Sterling Heights, Michigan). ImageJ software (Schneider et al. 2012) was used to measure the distance between annual otolith rings, and each otolith was aged and compared by two readers to reduce human error. The readers produced a consensus on estimated age for each White Sucker.

Back-calculated length at age was determined by using otolith annulus measurements to estimate annual somatic growth (i.e., the Fraser–Lee method; Everhart et al. 1975),

$$L' = C + \left(\frac{O'}{O}\right)(L - C),$$

where L' is the estimated length of an individual at a given age; C is the correction factor, which includes the fish size at

TABLE 1. Characteristics of Maine lakes from which White Suckers were sampled. Lake pairs (A, B, and C) included one lake that was open to harvest (harvested) and a similar lake that was closed to harvest (reference). "Years harvested" refers to the years in which permits were issued for White Sucker harvest. "Fish community" refers to the type of fish community in the lake (cold = lakes in which maximum mean monthly temperature [maxtemp] does not exceed 20°C; warm = lakes in which maxtemp does exceed 20°C).

Lake	Lake type	Harvest pressure	Years harvested	Area (ha)	Maximum depth (m)	Mean depth (m)	Fish community
			Pair A				
Unity Pond	Harvested	High	1994–2014	1,023	12.5	6.7	Warm
Chemo Pond	Reference	Minimal	2009	463	7.3	4.0	Warm
			Pair B				
Millinocket Lake	Harvested	High	2006–2014	1,093	16.5	6.7	Cold
Cold Stream Pond	Reference	Closed	None	1,468	31.7	12.2	Cold
			Pair C				
Graham Lake	Harvested	High	2006–2014	3,182	14.3	5.2	Warm
Pushaw Lake	Reference	Closed	None	2,046	8.5	3.4	Warm

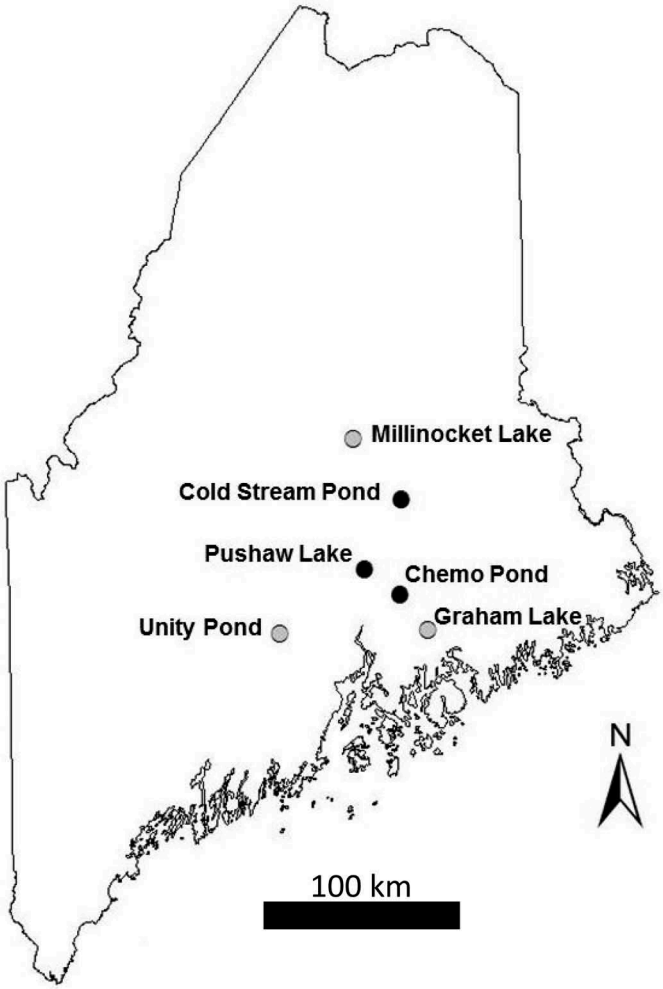

FIGURE 1. Map of Maine lakes where White Suckers were captured during April–May 2014. Gray circles represent lakes that were open to harvest; black circles represent lakes that were closed to harvest. Lakes were paired based on lake size and depth (pair A = Unity Pond and Chemo Pond; pair B = Millinocket Lake and Cold Stream Pond; pair C = Graham Lake and Pushaw Lake).

otolith formation (11 mm FL in White Suckers; Long and Ballard 1976); O' is the length of the annulus at a given age; O is the total length of the otolith; and L is the TL of the individual at the time of capture.

In the mid-North American range of their distribution, White Suckers reach sexual maturity at 2–6 years of age (Munkittrick and Dixon 1988; Thompson and Beckman 1995; Wakefield and Beckman 2005). For this study, we identified mature individuals as those with fully developed gonads. We were not able to determine the sex of nonspawning individuals due to indistinguishable gonads ($n = 57$; these individuals were not included in the analysis). The back-calculated length-at-age estimates of mature individuals were used to generate von Bertalanffy growth curves for each lake and each sex,

$$L_t = L_\infty \left[1 - e^{-K(t-t_0)}\right],$$

where L_t is the length at time t; L_∞ is the asymptotic length; K is the growth coefficient, indicating how quickly growth slows with age; and t_0 is the theoretical age at which length is zero (Trippel and Harvey 1991; Guy and Brown 2007). Growth parameters (L_∞, K, and t_0) were then compared between sexes and paired lakes to assess growth differences, as indicated by a lack of overlap in 95% confidence intervals (Zar 1999).

Mortality estimation.—Catch per lake was pooled from all gear to estimate mortality. For each lake, we conducted a linearized catch curve analysis using a peak-plus approach with the Robson–Chapman maximum-likelihood method of survival estimation (Guy and Brown 2007; Smith et al. 2012). Given the estimated survival rate, we then estimated the annual mortality rate (A) for each lake.

Fecundity estimation.—White Suckers are determinate spring spawners and have been found to reproduce in nonconsecutive years if environmental conditions limit available surplus energy (Geen et al. 1966; Trippel and Harvey 1989; Doherty et al. 2010). As outlined by Trippel and Harvey (1987), immature individuals or ovaries with ova suggestive of partial spawning were not included in the analysis. The gonad mass of mature females was measured to compute the gonadosomatic index (GSI), which characterizes energy storage in the gonads (Munkittrick and Dixon 1988):

$$\text{GSI} = \frac{\text{Gonad mass}}{\text{Total body mass}} \times 100.$$

Using the procedures described by Barbin and McCleave (1997), the ovaries of each gravid female ($n = 509$) were fixed with 2% acetic acid. Solutions were periodically agitated over 7 d until the ova separated from ovarian connective tissue. Three 5-mL aliquots from a well-mixed suspension were pipetted from the solution. Pipetted ova were placed on a petri dish, and an image was recorded for subsequent counts. The three subsamples were averaged and volume corrected to produce an overall estimate of the number of ova in the ovaries.

Statistical analyses.—Due to nonnormal distributions of TL (for two lakes), age, and fecundity, we adopted a conservative approach and tested all hypotheses nonparametrically. Harvested lakes and reference lakes were first nested to investigate differences in median size, median age, and median GSI ($\alpha = 0.05$). The Kolmogorov–Smirnov (K–S) two-sample test was used to compare frequency distributions, while the Kruskal–Wallis (K–W) test was used to compare medians between the nested lakes (i.e., for the response variables: size, age, fecundity, and GSI; Guy and Brown 2007). After the nested comparison, males and females were then analyzed separately due to sexual dimorphism. We used a series of paired lake comparisons for

TABLE 2. Dates of capture and FL ranges (mm) of White Suckers caught in each gear type (trap net; rigid, single-door, XL-fish trap with extension wings [trap with wings]; lobster pot; hoop net; or hand-made trap; see Methods) within each Maine lake during 2014. Lake pairs (A, B, and C; described in Table 1) included one lake that was open to harvest (harvested) and a similar lake that was closed to harvest (reference). "Sites" refers to the number of locations where gear was set in the tributaries; "date of capture" refers to the day on which fish were collected from the gear (i.e., gear was set the day before capture). Numbers in parentheses are the total numbers of individuals caught per gear type. A Kolmogorov–Smirnov two-sample test comparing FLs of fish caught by the gear types within each lake was conducted to assess gear bias (shared letters indicate similar size distributions at α = 0.05).

Lake type	Sites	Date of capture	Trap net	Trap with wings	Lobster pot	Hoop net	Hand-made trap
				Pair A			
Harvested	1	Apr 23–24					246–417 (282)
Reference	2	Apr 23–May 9		183–470 (52) z		87–319 (73) y	361–462 (17) z
				Pair B			
Harvested	1	May 10–14		217–432 (120)			
Reference	2	May 3–16	360–525 (122) z	366–449 (6) y			
				Pair C			
Harvested	2	Apr 3–May 1		190–470 (66) z	268–448 (64) y		
Reference	2	Apr 24–28	98–506 (153) z	197–404 (21) y			

each sex to investigate the same parameters used for the nested analysis. Size bias from gear types was also assessed with the K-S test when multiple gears were used in a single lake. Analyses were performed by using the "fishmethods" package in R version 3.2.3 (Nelson 2015).

RESULTS

Between 120 and 282 White Suckers (total n = 976) were collected from each of the six lakes. Individuals from reference lakes were generally larger than those from harvested lakes (in both the nested comparison and the paired lake comparisons for each sex). Each harvested lake had a different size distribution than its paired reference lake (all $P < 0.001$; Figure 2; Table 3), with the exception of males from pair C (K–S test: D-statistic = 0.26, P = 0.160). Both males and females from all harvested lakes had lower median sizes than fish from the corresponding reference lakes (K–W test: all $P < 0.05$; Tables 3, 4). Size distributions of males and females also differed at all of the study sites (K–S test: all $P <$ 0.001). Median size of female White Suckers was larger than that of males at all sites (Table 4).

Fish were generally older in closed lakes than in harvested lakes (in both the nested comparison and the paired lake comparisons for each sex). Each harvested lake had a different age distribution than its paired reference lake ($P < 0.001$; Figure 3; Table 3) with the exception of males from pair C (K–S test: D-statistic = 0.23, P = 0.343). In general, males and females from harvested lakes had younger median ages than those from reference lakes (K–W test: P < 0.050; Tables 3, 4). The maximum observed age was lower in harvested lakes than in reference lakes (pair A: 9 versus 15 years; pair B: 16 versus 26 years; pair C: 12 versus 22 years). The annual mortality rate A estimated for each lake based on catch curves differed within each lake pair (Table 5). Harvested lakes had more than twofold higher estimated A-values than their corresponding reference lakes. The harvested lake in pair A had the highest A (67.1 ± 5.2% [mean ± SE]) among all sites sampled (Table 5).

Sampling equipment in this study was used opportunistically, and although we did not expect large differences in size selectivity of the gear, there were detectable differences among methods. When comparing the distribution of fish sizes caught by different gear types within lakes (K–S test), all gears produced different distributions ($P < 0.05$), with the exception of the XL-fish trap with extension wings and the hand-made trap at the reference lake in pair A (K–S test: D-statistic = 0.3, P = 0.139; Table 2). It is important to note that some gear comparisons were hampered by small sample sizes within lakes (e.g., hand-made trap in the pair-A reference lake: n = 17; XL-fish trap with wings in the pair-B reference lake: n = 6; Table 2). The hoop net, trap net, and XL-fish trap with wings generally captured smaller-sized individuals. These methods were used in combination with other gear at all sites except the harvested lake in pair A (Table 2). Fish were caught at two different sites within each lake except the harvested lakes belonging to pair A and pair B.

Fish from harvested lakes had lower median fecundity than those from paired reference lakes (K–W test: $P < 0.001$; Figure 4; Tables 3, 6). Fish from harvested lakes also had lower median GSIs than fish from the corresponding reference lakes (K–W test: $P < 0.001$; Tables 3, 6). All paired sites had significantly different distributions of GSI (K–S test: $P < 0.001$), which was also found in the nested lake comparison. There were some differences in parameters estimated from the von Bertalanffy growth curves for paired lakes, as evidenced by nonoverlap in SEs (Figures 5, 6; Table 7). The K-values for both males and females in reference lakes were smaller than those in harvested lakes (Table 7), with

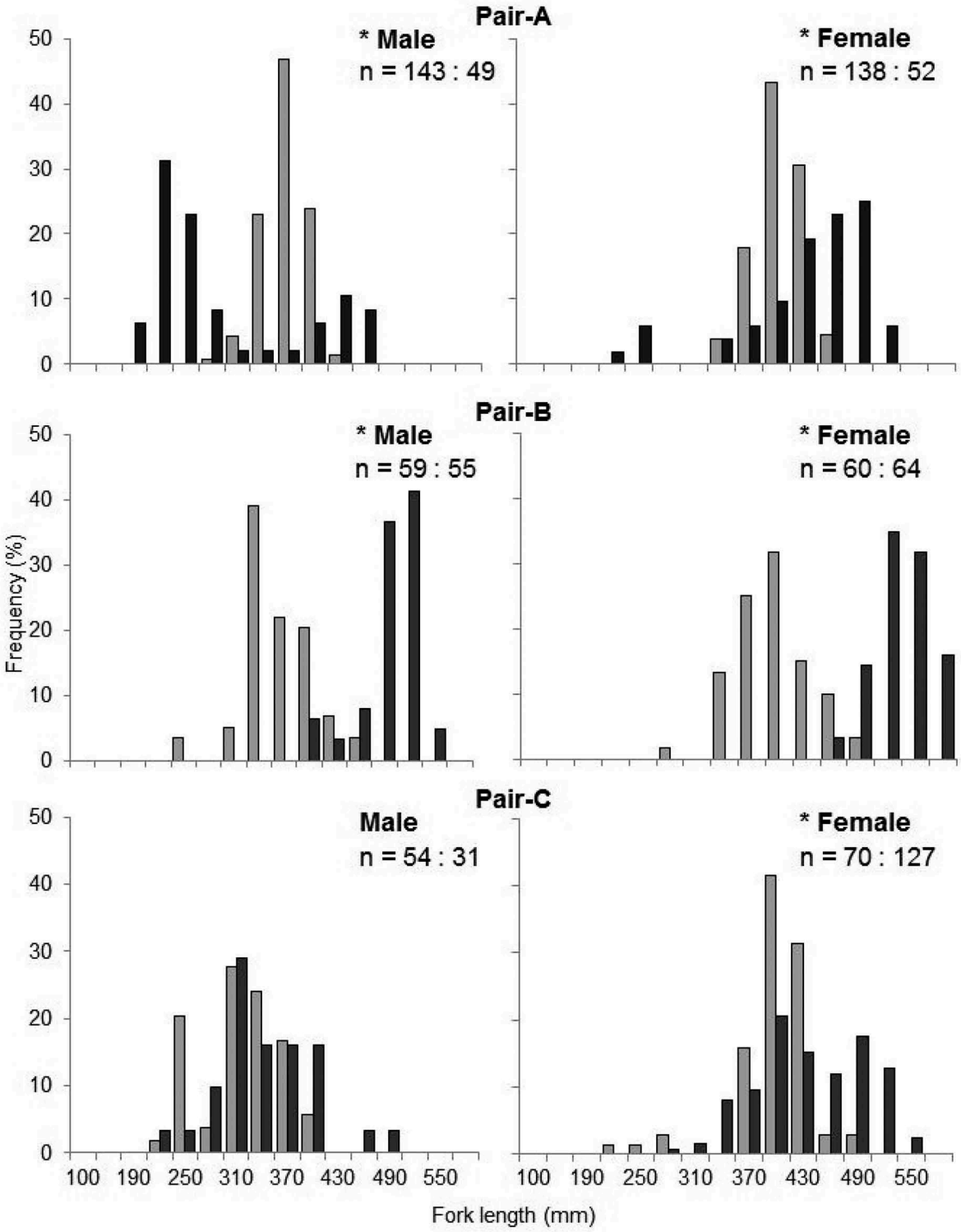

FIGURE 2. Size (mm FL) distributions of male and female White Suckers captured from lakes in Maine (n = number of fish aged from harvested lakes [gray bars]: reference lakes [black bars]). Refer to Table 1 for lake descriptions. Asterisks indicate that distributions significantly differed between harvested and reference lakes ($P < 0.001$).

TABLE 3. Results of analyses on demographic data for White Suckers sampled from lakes in Maine during 2014 (α = 0.05 for all tests; GSI = gonadosomatic index). The Kolmogorov–Smirnov two-sample test (K–S test; *D*-statistic) compared frequency distributions between nested lakes (harvested and reference) and lake pairs (A, B, and C; described in Table 1). The Kruskal–Wallis test (K–W test; *H*-statistic) compared medians between paired lakes. "Combined" represents the combined results for males and females; significant tests are denoted by asterisks (**P* < 0.05, ***P* < 0.01, ****P* < 0.001).

	K–S test			K–W test		
Group	Combined	Male	Female	Combined	Male	Female
			FL (mm)			
Nested	0.5***			150.9***		
Pair A		0.7***	0.6***		22.9***	28.5***
Pair B		0.9***	0.9***		84.0***	85.9***
Pair C		0.3	0.4***		3.8*	15.4***
			Age (years)			
Nested	0.5***			211.0***		
Pair A		0.4***	0.6***		8.4**	45.7***
Pair B		0.9***	0.8***		78.7***	64.1***
Pair C		0.2	0.3***		3.9*	21.4***
			GSI			
Nested	0.2***			32.2***		
Pair A			0.4***			19.0***
Pair B			0.7***			62.1***
Pair C			0.3***			13.3***
			Fecundity (total ovum count)			
Nested	0.5***			115.2***		
Pair A			0.6***			48.9***
Pair B			0.9***			29.0***
Pair C			0.5***			46.4***

TABLE 4. Median biological characteristics of mature female (190–525 mm FL) and mature male (173–490 mm FL) White Suckers sampled from lakes in Maine. Lake pairs (A, B, and C; described in Table 1) included one lake that was open to harvest (harvested) and a similar lake that was closed to harvest (reference). Upper and lower 95% confidence limits are listed in parentheses.

Pair	Lake type	*n*	FL (mm)	Somatic mass (g)	Age (years)
			Females		
A	Harvested	134	363 (357, 367)	633 (603, 660)	4 (4, 4)
	Reference	47	404 (386, 421)	849 (655, 950)	7 (5, 8)
B	Harvested	14	355 (341, 365)	508 (441, 550)	5 (5, 6)
	Reference	56	489 (469, 496)	1,566 (1,475, 1,654)	13 (12, 15)
C	Harvested	55	365 (358, 372)	571 (524, 622)	6 (6, 6)
	Reference	122	392 (372, 405)	742 (653, 834)	8 (7, 8)
			Males		
A	Harvested	141	330 (324, 335)	496 (481, 523)	4 (4, 4)
	Reference	49	213 (204, 236)	118 (100, 176)	3 (3, 3)
B	Harvested	57	320 (312, 335)	368 (342, 434)	5 (5, 5)
	Reference	60	456 (443, 464)	1,375 (1,293, 1,470)	12 (12, 15)
C	Harvested	54	283 (275, 296)	281 (243, 312)	4 (3, 4)
	Reference	29	298 (285, 326)	332 (272, 492)	5 (4, 5)

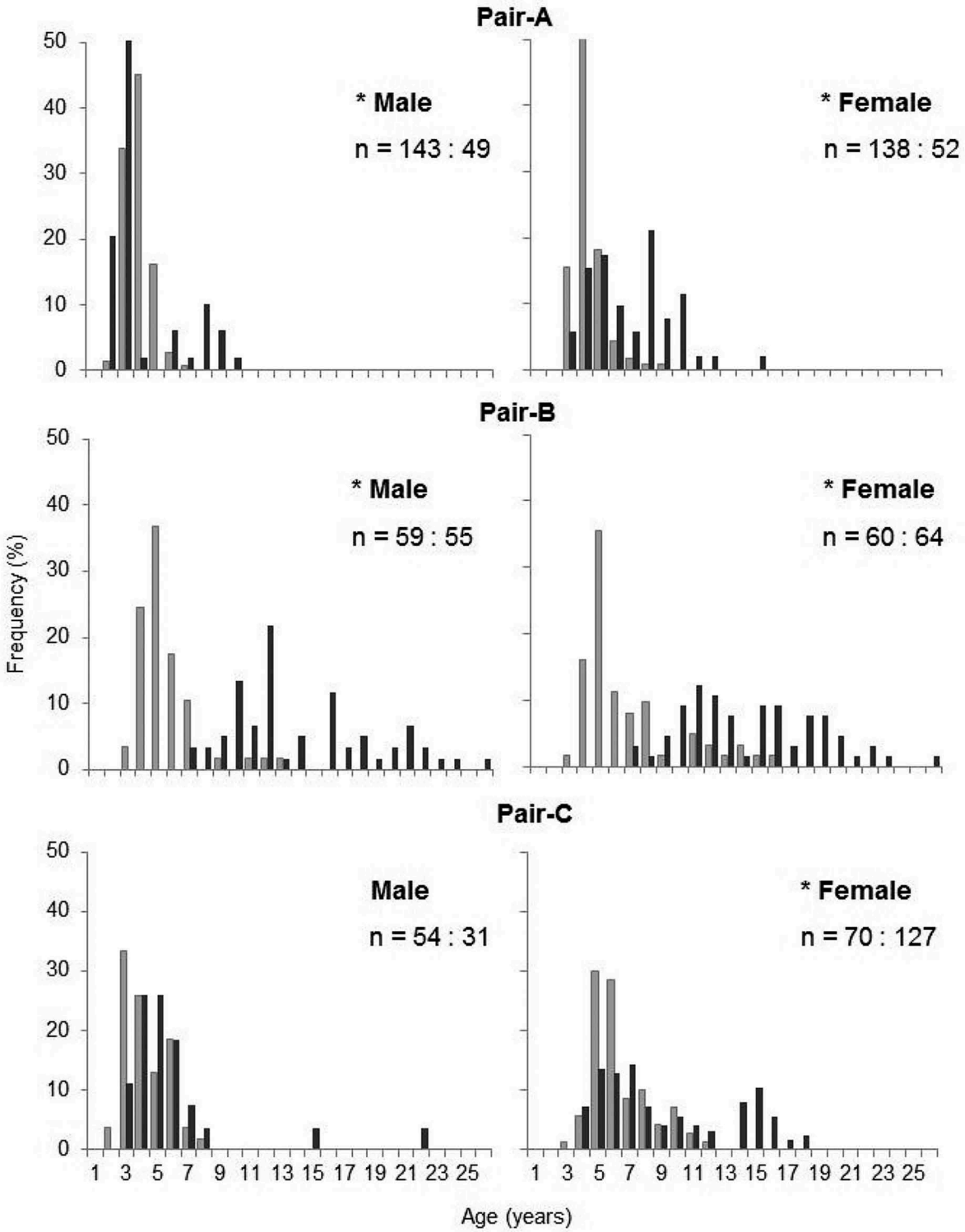

FIGURE 3. Age distributions of male and female White Suckers captured from lakes in Maine (n = number of fish aged from harvested lakes [gray bars]: reference lakes [black bars]). Refer to Table 1 for lake descriptions. Asterisks indicate that distributions significantly differed between harvested and reference lakes ($P < 0.001$).

TABLE 5. Annual mortality estimates for mature White Suckers in Maine lakes, as obtained using a peak-plus approach with the Robson–Chapman maximum-likelihood method of survival estimation. Lake pairs (A, B, and C; described in Table 1) included one lake that was open to harvest (harvested) and a similar lake that was closed to harvest (reference). Age is the range of mature ages, fully recruited age is the range of ages that are fully recruited to the gear, and *A* is estimated annual mortality. Upper and lower 95% confidence limits are listed in parentheses.

Lake type	FL (mm)	Age (years)	Fully recruited age (years)	*A* (%)
		Pair A		
Harvested	246–417	2–9	4–9	67.1 (61.9, 72.3)
Reference	173–470	3–15	3–15	25.2 (20.7, 29.7)
		Pair B		
Harvested	224–432	3–16	5–16	35.5 (29.7, 41.5)
Reference	360–525	7–26	12–26	23.1 (18.0, 28.2)
		Pair C		
Harvested	190–448	2–12	6–12	45.2 (36.5, 53.9)
Reference	198–506	2–22	5–22	18.3 (15.5, 21.1)

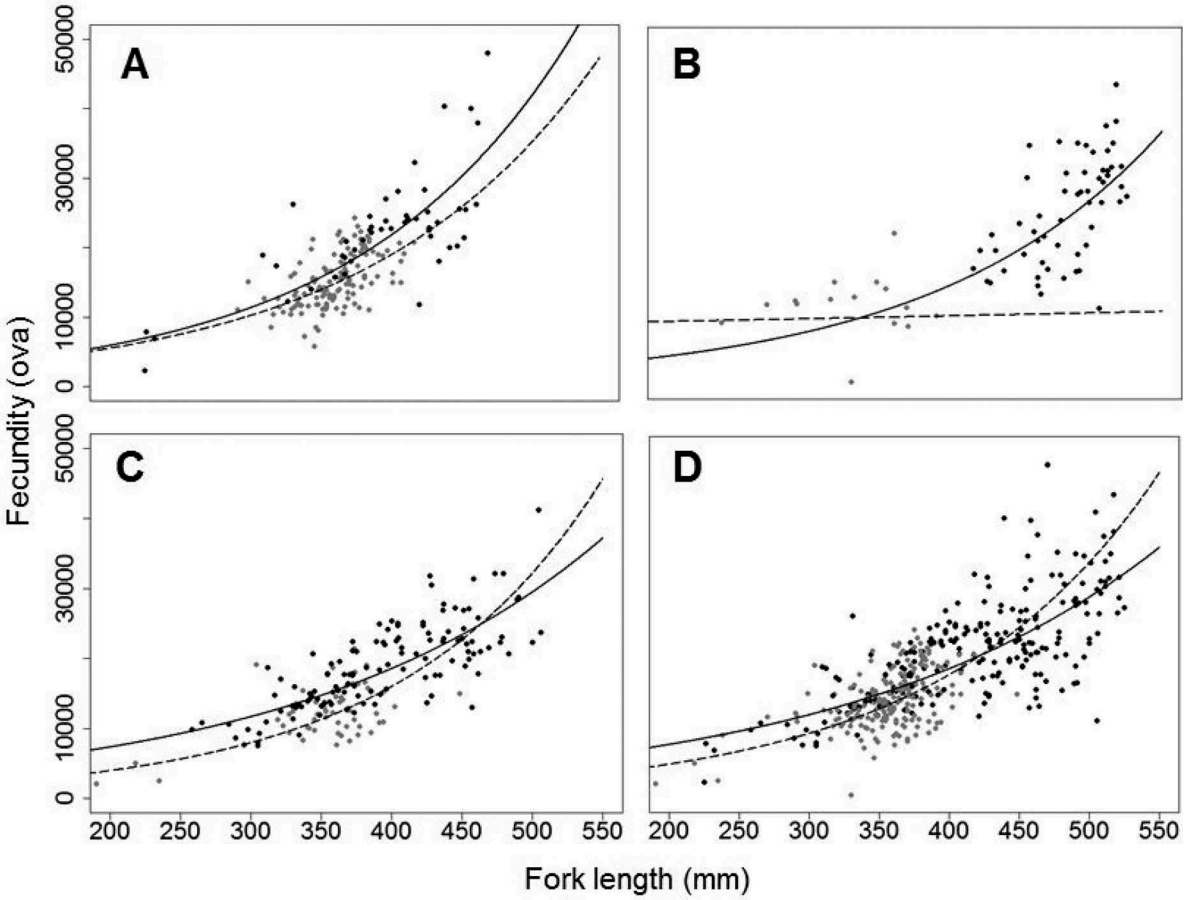

FIGURE 4. Relationships between fecundity (total ovum count) and FL (mm) of female White Suckers captured from paired lakes (gray symbols, dashed lines = harvested lakes; black symbols, solid lines = reference lakes) in Maine: **(A)** pair A, **(B)** pair B, **(C)** pair C, and **(D)** all lakes combined. Refer to Table 1 for lake descriptions.

TABLE 6. Median reproductive characteristics of mature female (190–525 mm FL) White Suckers sampled from lakes in Maine (GSI = gonadosomatic index). Lake pairs (A, B, and C; described in Table 1) included one lake that was open to harvest (harvested) and a similar lake that was closed to harvest (reference). Upper and lower 95% confidence limits are listed in parentheses.

Lake type	*n* females	Gonad mass (g)	GSI (%)	Fecundity (total ovum count)
		Pair A		
Harvested	134	86 (81, 91)	12 (12, 12)	15,100 (14,340, 15,720)
Reference	47	129 (95, 143)	14 (13, 14)	22,650 (20,940, 24,120)
		Pair B		
Harvested	14	45 (30, 51)	10 (7, 10)	12,050 (10,033, 13,984)
Reference	56	206 (178, 229)	12 (11, 12)	26,550 (21,930, 30,060)
		Pair C		
Harvested	55	74 (58, 78)	11 (10, 11)	12,240 (10,984, 13,550)
Reference	122	94 (83, 111)	12 (11, 12)	18,700 (17,670, 20,820)

the exception of males from pair C. Fish (both males and females) from the reference lake in pair B had larger estimated L_∞ values than the harvested lake in that pair, whereas males showed similar results between the lakes in pair A. The L_∞ pooled for both sexes and lakes was estimated to range from 373 to 686 mm (Table 7).

DISCUSSION

Because our study was based on opportunistic sampling, we used a weight-of-evidence approach for inferring demographic differences between selected pairs of lakes that were subjected to differing harvest pressure. The results of our work demonstrate that White Suckers in harvested populations had smaller median sizes, younger ages, and lower fecundity for a given mass than those in similar lakes that were closed to harvest. Age distributions of male and female White Suckers from harvested populations were narrower and shifted toward younger age-classes compared with reference populations (except males in pair C, although the lack of difference could be due to low sample sizes; harvested lake: $n = 31$; reference lake: $n = 54$). Harvested populations were dominated by younger, smaller fish. In combination, these pervasive patterns suggest the existence of harvest-driven effects through age selectivity and size selectivity, as indicated by the absence of larger and older individuals within harvested populations. As predicted, reference populations had greater ranges in fish age that were likely due to the absence of size-selective harvest.

It is important to note several limitations of the study based on the design and approach. There was no quantifiable way to identify and sample lakes based on quantified rates of harvest mortality. Furthermore, we were unable to standardize the gear given that a major part of the project was to collaborate with commercial harvesters to opportunistically collect fish from assigned lakes (other than minimum mesh size requirements, there are few restrictions on gear type in the fishery). There were potential confounding effects of gear (apparent in the bimodal distribution for size ranges at reference lakes in pairs A and C; Table 2), low sample size, and strong cohort effects. However, despite these limitations, the data strongly indicate a significant influence of commercial harvest.

The range in A for reference lakes (18.3–25.2%) was comparable to reported natural mortality rates of age-7 and older White Suckers, although those values ranged widely—from 0.3% in Colorado (Trippel and Harvey 1987) to 30% in Ontario (McPhee 2007). The study lakes are located within the same latitudinal range, which gives us confidence that our estimates of A are reasonable representations of what might be expected in Maine. Many environmental factors affect mortality rates for individual waters, such as food availability, competition with other species, water chemistry, regional climate, and elevation. Given the scope of this study, we were unable to test for these influences, but our paired study design largely controlled such variability when inferring potential additive effects of harvest.

Indeed, consistent with the observed age distributions for harvested White Sucker populations, the data suggest that harvest had a considerable additive effect on natural mortality for all lakes that were open to harvest. Estimated A from harvested lakes was high, ranging from 35.5% to 67.1%. Within lake pairs, values of A estimated for the harvested lakes were 2.0- to 2.8-fold higher than those estimated for the closed lakes (Table 5). High mortality can affect population persistence and may create a risk of population collapse (Miranda 2002). Although we have little information on the extent of harvest, we can infer that current harvest levels are greatly increasing mortality rates and truncating age distributions of White Suckers in a biologically relevant fashion.

White Suckers from reference lakes produced more ova on average than those in harvested lakes. The observed differences in median fecundity were likely due to differences in female size distributions between the paired lakes. White Suckers can produce 5,000–59,000 eggs during a spawning

season, with fish mass and fecundity exhibiting a positive correlation (Wakefield and Beckman 2005; McPhee 2007). In our study, the range in estimated fecundity was 2,066–48,000 ova per female. Fecundity is important information for assessing stock–recruitment relationships and the reproductive potential of a population (Koslow et al. 1995; McCarthy et al. 2008), but other demographic factors are also critical for population resilience. Older fish are more successful at egg production than young or newly matured fish (Trippel 1998; Winemiller 2005; Brunel 2010), and as expected, we observed higher ovum counts in large individuals.

We noted a difference in apparent age at maturity between the sexes for fish captured in this study. Males were observed to reproduce at age 2, while females began reproducing at age 3 (i.e., based on the presence of mature gonads). Our age-at-maturity estimates were consistent with observations reported in other studies (Beamish 1973; Munkittrick and Dixon 1988; Trippel and Harvey 1991). Male White Suckers mature earlier than females, whereas females often live longer (Chen and Harvey 1994; Wakefield and Beckman 2005; Smith et al. 2008). Size- or age-selective harvest might alter White Sucker maturity in Maine lakes, but due to our small sample sizes, we were unable to detect maturity differences between the paired populations we examined. Harvest-induced early maturity has been documented in a number of North Atlantic fish stocks, yet little is known about this phenomenon in freshwater stocks (Brunel 2010), and it remains an important research question to be explored for White Suckers and other freshwater species.

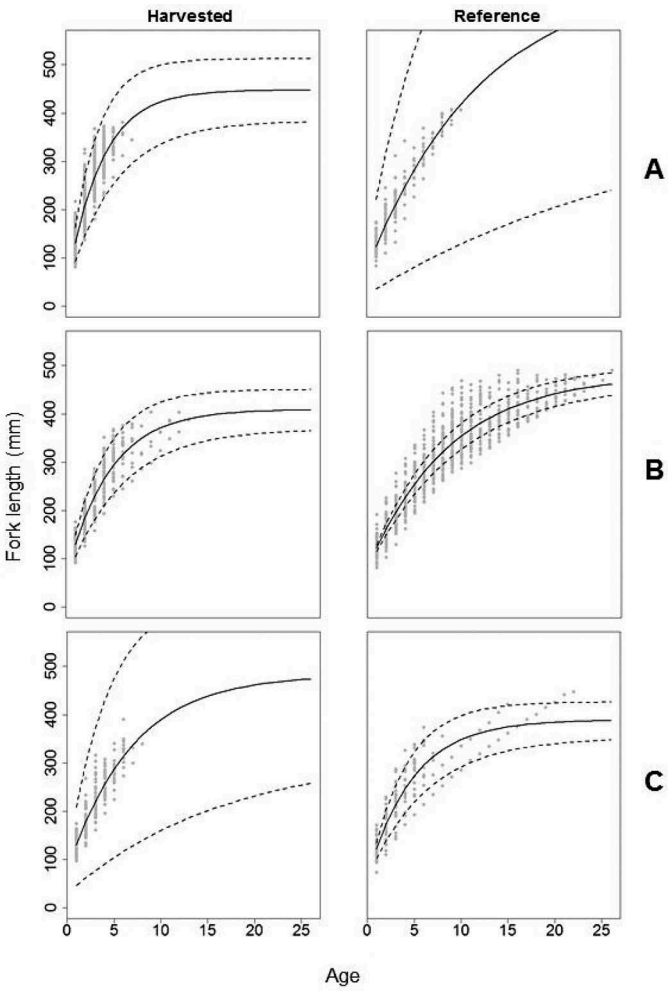

FIGURE 5. Von Bertalanffy growth curves generated from back-calculated measurements of otoliths from male White Suckers captured in Maine lakes. Lettering refers to lake pairs (A, B, and C), each of which included one lake that was open to harvest (harvested) and a similar lake that was closed to harvest (reference). Refer to Table 1 for lake descriptions. Dotted lines indicate 95% confidence bounds.

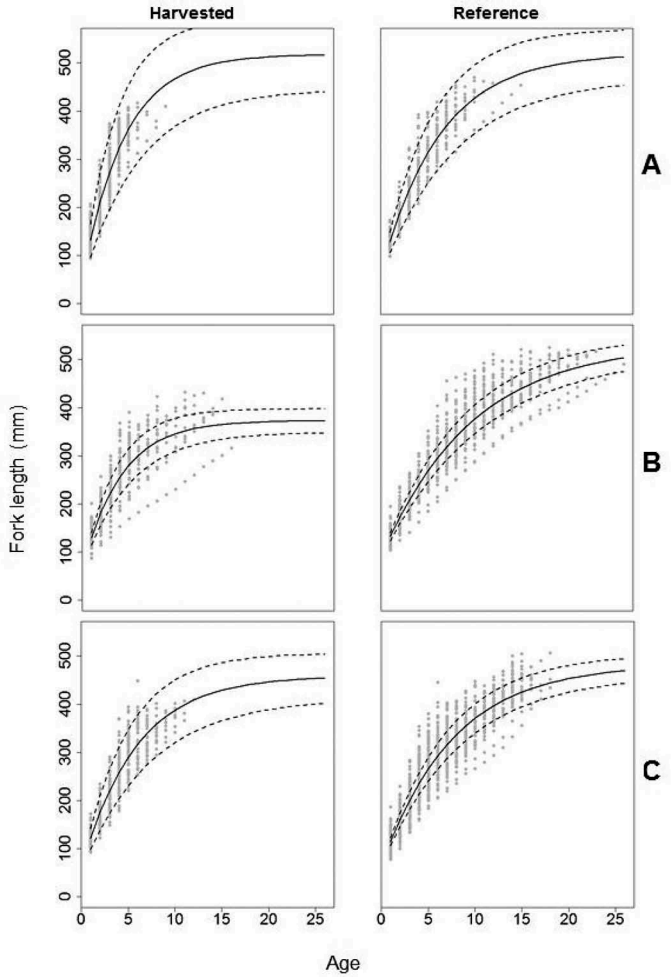

FIGURE 6. Von Bertalanffy growth curves generated from back-calculated measurements of otoliths from female White Suckers captured in Maine lakes. Lettering refers to lake pairs (A, B, and C), each of which included one lake that was open to harvest (harvested) and a similar lake that was closed to harvest (reference). Refer to Table 1 for lake descriptions. Dotted lines indicate 95% confidence bounds.

By generating von Bertalanffy curves and comparing parameters, we found some evidence for harvest-related differences in lifetime growth trajectories between paired lakes (Figures 5, 6; Table 7). The individual variation observed from the back-calculation of ages and growth trajectories was high and could have been driven by behavioral (feeding) or habitat use differences in individuals. This variation makes growth differences difficult to assess and could also be an artifact of the modest sample size obtained for each age-class within each lake.

The White Sucker commercial fishery is young compared to other commercial fisheries; MDIFW has only been issuing permits for the last 25 years. Anecdotal evidence (e.g., personal communication with current harvesters) suggests that White Suckers in some areas of Maine have been commercially harvested for up to 40 years. The relatively recent fishing pressure is notable for this long-lived species. We observed fish as old as 26 years; therefore, as many as 10 generations and as few as 2 generations may have passed since significant harvest began in these waters (using a rough estimate of age 5 as the earliest common age of maturation). Although this may be enough time for the emergence of important evolutionary responses to harvest, it may be too early to easily detect such changes.

Based on detectable differences in White Sucker growth for some of our lake pairs, it is possible that harvest is having a major selective effect on the life history traits of these populations. There is also strong evidence of selective effects in other demographic traits, such as size, age, and fecundity. We report a markedly greater A for White Suckers in harvested lakes than in paired reference lakes. Because there was no information on the number of permitted harvesters at each waterbody, we were unable to quantify harvest effort or to determine whether harvest might pose a risk to population persistence. Since White Suckers are long lived, the presence of larger (often older) individuals may be critical for the continued survival of younger age-classes. Further monitoring of this species and closer inspection of the fishery (e.g., collecting

TABLE 7. Von Bertalanffy parameters estimated based on back-calculated measurements from the otoliths of White Suckers sampled in Maine (L_∞ = theoretical maximum [asymptotic] length; K = growth coefficient describing the rate at which L_∞ is approached; t_0 = theoretical age [years] at zero length; FL range = size of fish used in back-calculations; n = number of fish used in the analysis). Lake pairs (A, B, and C; described in Table 1) included one lake that was open to harvest (harvested) and a similar lake that was closed to harvest (reference). Upper and lower 95% confidence limits for parameters are listed in parentheses.

Pair	Lake type (sample size)	L_∞	K	t_0	FL range (mm)
		Females			
A	Harvested	518	0.23	–0.30	291–417
	(n = 138)	(481, 618)	(0.20, 0.26)	(–0.38, –0.22)	
	Reference	520	0.16	–0.78	203–470
	(n = 52)	(494, 546)	(0.14, 0.18)	(–0.89, –0.67)	
B	Harvested	373	0.24	–0.75	238–432
	(n = 60)	(361, 385)	(0.22, 0.26)	(–0.88, –0.62)	
	Reference	533	0.10	–1.74	416–525
	(n = 60)	(522, 544)	(0.09, 0.11)	(–1.84, –1.64)	
C	Harvested	459	0.17	–0.78	190–448
	(n = 70)	(435, 483)	(0.15, 0.19)	(–0.89, –0,67)	
	Reference	483	0.13	–1.05	258–506
	(n = 127)	(472, 494)	(0.12, 0.14)	(–1.12, –0.98)	
		Males			
A	Harvested	447	0.28	–0.23	246–381
	(n = 143)	(414, 480)	(0.24, 0.32)	(–0.32, –0.14)	
	Reference	686	0.08	–1.41	173–408
	(n = 49)	(543, 829)	(0.05, 0.11)	(–1.64, –1.18)	
B	Harvested	410	0.22	–0.72	224–404
	(n = 59)	(389, 431)	(0.19, 0.25)	(–0.84, –0.60)	
	Reference	483	0.12	–1.56	360–490
	(n = 55)	(473, 493)	(0.11, 0.13)	(–1.66, –1.46)	
C	Harvested	483	0.15	–1.13	206–390
	(n = 54)	(399, 567)	(0.10, 0.20)	(–1.38, –0.88)	
	Reference	389	0.21	–0.81	198–447
	(n = 31)	(370, 408)	(0.18, 0.24)	(–0.98, –0.64)	

information on gears used, effort, and catch totals during the season) would be instructive for assessing management objectives.

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