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Lakewide Estimates of Alewife Biomass and Chinook Salmon Abundance and Consumption in Lake Ontario, 1989–2005: Implications for Prey Fish Sustainability

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Abstract.—Stocking levels of Chinook salmon *Oncorhynchus tshawytscha* for Lake Ontario have been highly controversial since the early 1990s, largely because of uncertainties about lakewide abundance and rates of prey consumption. Previous estimates have focused on years before 1995; since then, however, the Lake Ontario ecosystem has undergone substantial changes, and there is new evidence of extensive natural recruitment. Presented here are new abundance estimates of Chinook salmon and alewives *Alosa pseudoharengus* in Lake Ontario and a reevaluation of the potential risk of alewife population collapse. We found that Lake Ontario has been supporting, on average (1989–2005), 1.83×10^6 (range, 1.08×10^6 to 3.24×10^6) Chinook salmon of ages 1–4, amounting to a mean annual biomass of 11.33×10^3 metric tons (range, 5.83×10^3 to 23.04×10^3 metric tons). During the same period (1989–2005), the lake supported an alewife biomass of 173.66×10^3 metric tons (range, 62.37×10^3 to 345.49×10^3 metric tons); Chinook salmon of ages 1–4 consumed, on average, 22% (range, 11–44%) of the alewife biomass annually. Because our estimates probably underestimate total consumption and because Chinook salmon are only one of several salmonine species that depend on alewives, predation pressure on the Lake Ontario alewife population may be high enough to raise concerns about long-term stability of this predator–prey system.

The open-lake recreational fisheries of the Great Lakes are dominated by Pacific salmonines, of which the Chinook salmon *Oncorhynchus tshawytscha* is the most abundant and highly valued species caught by anglers; Chinook salmon also consume the most prey (Stewart et al. 1981; Rand and Stewart 1998a, 1998b). The Pacific salmonines were intentionally stocked in the Great Lakes beginning in the late 1960s to control the overabundant populations of nonindigenous alewives *Alosa pseudoharengus* and to create a recreational sport fishery (Tanner 1971). In Lake Ontario, the sport fishery for stocked salmon and trout grew quickly and became an economic mainstay of many local and regional communities (Talhelm 1988; Connelly et al. 1999). In the early 1990s, concern for the sustainability of prey fish populations arose as the annual release of hatchery-reared Chinook salmon began to exceed 6×10^6 fish (Jones et al. 1993). In response, the numbers stocked in Lake Ontario were reduced after 1992 to lower predatory demand by 50%. In 1997, however, the number of Chinook salmon stocked annually was increased by about 30% after a second review of the prey fish population found it to be more resilient than previously thought (Brandt et al. 1996).

Previous attempts at reconciling predatory demand with prey fish abundance in Lake Ontario concentrated on the years before 1995 (Jones et al. 1993; Rand and Stewart 1998b). Since 1995, changes have occurred in the alewife population and additional knowledge has been acquired on Chinook salmon recruitment and life

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history. Adult alewife numbers were significantly lower during 1996–2006 than during 1978–1995; the condition (Fulton's condition factor, *K*) of adult alewives in 2003–2006 was significantly higher than in 1981–2002 but significantly lower than in 1976–1980 (O'Gorman et al. 2008). Alewife *K* is directly related to energy density (Rand et al. 1994; Madenjian et al. 2006), and declines in alewife average size and energy density in Lake Ontario during the 1980s contributed to an increase in Chinook salmon daily consumption from 1.5 prey fish/d to 3.7 prey fish/d (Rand et al. 1994; Rand and Stewart 1998a).

Previous estimates of alewife consumption by Chinook salmon in Lake Ontario were based on the assumption that there was minimal, if any, recruitment of wild-spawned Chinook salmon to the adult population and that the Chinook salmon population consisted predominately of hatchery-origin fish. Although natural reproduction in Lake Ontario tributaries was recorded as early as the 1970s (Johnson and Ringler 1981), only recently has there been evidence of extensive natural reproduction by Chinook salmon throughout the Lake Ontario drainage (e.g., Berends 2004; Everitt 2006; Smith et al. 2006). One study estimated that well over 5×10^6 parr were produced in a single year in the Salmon River, New York, alone (Everitt 2006), but the extent of smolt survival and the contribution to the lakewide population were only very recently evaluated by Connerton et al. (2009), who found that, on average, 62% (95% confidence interval, 48.4–75.6%) of age-3 Chinook salmon were of wild origin between 1992 and 2005. Clearly, these new findings about the potential magnitude of natural recruitment raise doubts about past estimates of Chinook survival and consumption of alewives in Lake Ontario.

Additionally, past bioenergetic-based consumption estimates assumed that Chinook salmon occupied water of 11°C during the summer months (Stewart and Ibarra 1991). In contrast, thermal histories determined recently from analyses of the oxygen-18 isotope (δ^{18}O) in otoliths suggest that midsummer water temperatures occupied by Chinook salmon in Lake Ontario may reach 19–20°C (Wurster et al. 2005). More recently, Stewart and Bowlby (2009), using angler depth at catch data, estimated that Chinook salmon routinely occupied water temperatures up to 14°C. Collectively, these two recent estimates certainly suggest that Chinook salmon are occupying waters warmer than previously thought and that past bioenergetic consumption estimates were biased low because warmer temperatures decrease the conversion efficiency of larger fish by increasing metabolic costs. Wurster et al. (2005) suggested that previous consumption estimates may have underestimated the quantity of alewives eaten by Chinook salmon by about 20% relative to previously used cooler temperatures (i.e., 11°C; Stewart and Ibarra 1991).

Collectively, the new information on alewife numbers and *K*, the magnitude of Chinook salmon natural recruitment, and the thermal regimes used by Chinook salmon prompted our evaluation of the magnitude of Chinook salmon predation on the Lake Ontario alewife population to assess the potential risk of alewife population collapse and to facilitate more informed stocking and management decisions. Our objectives were to (1) estimate the annual lakewide, age-specific abundance and biomass of Chinook salmon during 1989–2005, (2) use the calculated abundance and biomass estimates, in conjunction with observed Chinook salmon growth and changes in alewife condition (i.e., energy density as determined from *K*), to estimate annual consumption of alewives by Chinook salmon, (3) compare estimated alewife consumption by Chinook salmon with newly derived annual estimates of lakewide alewife biomass, and (4) compare past estimates of Chinook salmon consumption with our latest findings.

Methods

Age-specific Chinook salmon abundance and biomass.—Total age-specific Chinook salmon abundance (CA) was estimated as the sum of hatchery and wild fish in a given age-group (ages 1–4; 1989–2005):

$$\mathrm{CA}_{total,a} = \mathrm{CA}_{w,a} + \mathrm{CA}_{h,a}, \tag{1}$$

where $w =$ wild, $h =$ hatchery, and $a =$ age-group. Age-specific abundance of wild fish is estimated from equation (2), and that of hatchery fish is estimated from equation (3). The total annual standing stock of Chinook salmon in a given year was simply calculated as the sum of age-specific abundances. We use the term "age-group" rather than "age-class" because our calculations are based on a September–September year (due to available data) rather than the more traditional annulus to annulus (May–May) year, as was done in past estimates (e.g., Rand and Stewart 1998b).

Age-specific abundance of wild Chinook salmon was estimated through a simple algebraic expression of the number of hatchery fish (estimated by equation 3) and the estimated proportion (*P*) of wild and hatchery fish (Connerton et al. 2009; Figure 1):

$$\mathrm{CA}_{w,a} = \mathrm{CA}_{h,a} \times (P_{w,a}/P_{h,a}). \tag{2}$$

The age-specific abundance of hatchery fish was estimated as the product of abundance in the previous year (or number stocked, where $a = 0$) and age-specific

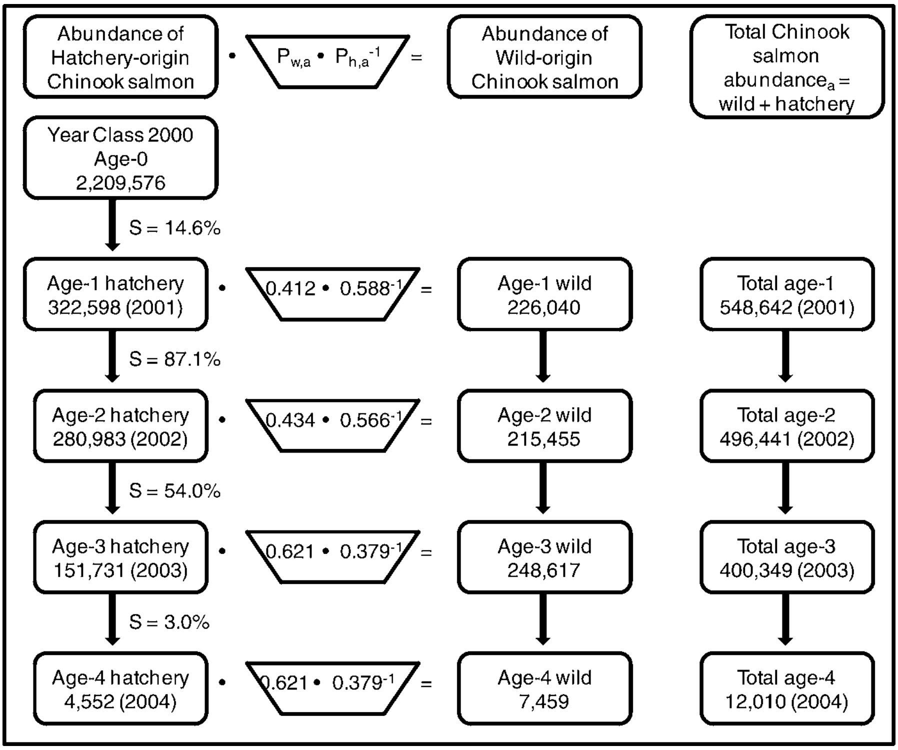

FIGURE 1.—Illustration of year-class and annual open-lake abundance estimates for hatchery- and wild-origin Chinook salmon in Lake Ontario. This example shows the survival rates (S) applied from stocking to age 4 for the 2000 year-class (equation 3), the derived wild proportion ($P_{w,a}$) of the open-lake stock (equation 2), and their summation, which results in the total age-specific abundance in the lake (equation 1), spanning 4 years.

survival rate ($S_{[a-1 \text{ to } a]}$; Figure 1):

$$\mathrm{CA}_{h,a} = (\mathrm{CA}_{h,a-1}) \times [S_{(a-1\,\mathrm{to}\,a)}]. \tag{3}$$

Details of how age-specific survival rates were estimated are provided briefly in the following section and more thoroughly in the Appendix. Data on the number of Chinook salmon stocked annually by New York and Ontario were obtained from New York State Department of Environmental Conservation (NYSDEC) reports (Eckert and Connerton 2007), and the annual age-specific proportions of wild fish were derived from Connerton et al. (2009). Where values for a given year or age-group were lacking (i.e., not provided in Connerton et al. 2009), we used the mean over all years of existing data (e.g., all but four year-classes of ages 1 and 2). Connerton et al. (2009) did not report the proportion of wild and hatchery age-4 fish, so by necessity, we assumed that the proportion of wild fish among age-4 Chinook salmon was the same as the age-3 proportion.

To calculate cohort biomass in September of each year (age- and year-specific biomass $B_{a,t}$, where t = year), we multiplied the estimated abundance by the age-specific and year-specific observed mean wet weight (g) of Chinook salmon. Total standing stock biomass in a given year was calculated as the sum of ages.

The mean weight at age of Chinook salmon in the open lake from 1985 to 2005 was constructed from three data sources: (1) data collected each September (1991–2005) by a creel survey conducted in the open lake (Eckert 2007), (2) data collected each September (1972–1986) by a gillnetting survey conducted in the mouth of the Salmon River (Wedge 1986), and (3) data collected each October (1986–2005) from fish returning to the Salmon River Hatchery (Bishop and Prindle 2007). Primarily, we used Eckert's (2007) data from 1991 to 2005 because they represent the maximum weight of Chinook salmon in the open lake before any weight loss by adults during upstream migration. For 1985–1986, we used Wedge's (1986) data because they were obtained at the beginning of the upstream migration. For 1987–1990, we predicted the weight at age for fish in the open lake during September from data collected at the Salmon River Hatchery; linear regressions were used to relate weight at the hatchery to weight in the open lake during 1991–2005 (r^2 range, 0.51 [age 1] to 0.87 [age 3]).

Hatchery Chinook salmon survival.—New age-specific survival estimates were calculated (Appendix) using a modified version of the approach utilized by Rand and Stewart (1998b), who based their survival estimates on the estimated age-specific cohort abundance (expressed as the sums of fish lost through harvest or death at each age for fish stocked in the Salmon River). Losses that were accounted for included U.S. and Canadian open-lake angler harvest, Salmon River angler harvest, and harvest at the Salmon River Hatchery. Assumptions of the original Rand and Stewart (1998b) model were no natural recruitment, equal survival for all stocking sites, and no straying from other stocking sites into the Salmon River.

We utilized the same approach as Rand and Stewart (1998b) but additionally accounted for (1) fish that died during the spawning run (i.e., fish not harvested by anglers or the hatchery; this estimate has exceeded angler harvest in some years; Everitt 2006; Appendix), and (2) the proportion of wild-origin fish in the population (Connerton et al. 2009). Survival estimates calculated here, however, are for hatchery-origin fish only because there were insufficient data (e.g., initial abundance) to calculate survival of wild-origin fish. It should additionally be made clear that our survival estimates are intended for the calculation of open-lake abundance in September and therefore include spawning losses, which occur in October and November of the previous year. Values thus computed are not directly comparable with those reported by Rand and Stewart (1998b). We accumulated sufficient data to estimate age-specific survival for the cohorts stocked in 2000–2004 (Appendix).

Chinook salmon gross consumption.—Gross consumption was calculated using a bioenergetic simulation (Stewart and Ibarra 1991) bounded by observed growth data. The bioenergetics model was programmed in Visual Basic interfaced with Microsoft Excel. The basic model format, equations, and coefficients were the same as those documented in other sources (Stewart and Ibarra 1991; Hanson et al. 1997). Essentially, total annual consumption (C) is the sum of energy required to achieve observed growth (G) and all losses (respiration R; specific dynamic action [SDA]; egestion F; and excretion U).

$$C = G + R + \mathrm{SDA} + F + U. \qquad (4)$$

The basic Wisconsin-style bioenergetics model is well known and highly documented (Kitchell et al. 1977; Stewart et al. 1983; Stewart and Ibarra 1991; Hanson et al. 1997), so further description here is unnecessary. The bioenergetics model ran on a daily time step for 21 years (1985–2005) and calculated consumption of a single average fish for ages 1–4 (e.g., three age-groups 1–2, 2–3, and 3–4 from September 15 of year t to September 14 of year $t + 1$). We did not model consumption for Chinook salmon age-group 0–1 because the switch to piscivory occurs late in the first year of life at an unknown—and probably highly variable—body size. Moreover, when Chinook salmon of this age-group do switch to a diet of fish, they mostly consume age-0 alewives, which were not included in the alewife abundance estimates (see next section). The Chinook salmon of age-group 1–2 began our simulation at approximately 16 months of lake age (i.e., their second September after entering the lake). The model was initialized with the beginning age-specific, year-specific mean weight (g; fish mass in the previous year) and the end weight (fish mass in the current year). The proportion of maximum consumption (Kitchell et al. 1977) was set to 0.01, and the model was run for 365 d and was repeated, incrementing the proportion of maximum consumption by 0.01 for each repetition until the final modeled weight was equal to or slightly greater than the observed end weight (modeled weight averaged <1% higher than the observed or target weight).

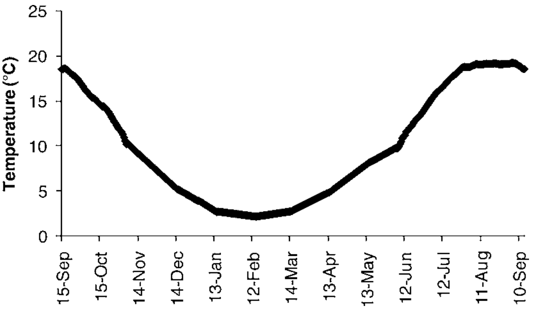

FIGURE 2.—Annual temperature profile used in all bioenergetics simulations for Lake Ontario. Data from June 6 through November 5 were derived from Wurster et al. (2005), and the remaining winter and spring data were derived from measurements at the Shoremount Municipal Water Treatment Plant located on the south shore of Lake Ontario.

We used the same 365-d temperature series for all years of the simulation (Figure 2) and assumed that preferred temperatures occurred somewhere in the water column and that the fish were able to move to those depth strata. Thus, we believe that the lack of interannual temperature variation had minimal influence on the results. The annual temperature profile we used was the average observed values occupied by Chinook salmon in Lake Ontario based on stable isotope analyses of otoliths (Wurster et al. 2005). Stable isotopes provide a time-integrated average; thus, we feel that these data provide the best available assessment of temperatures actually used by Chinook salmon. Wurster et al.'s (2005) temperature data set was for June 6 through November 5, the period when the lake is typically stratified. For the remaining winter and spring temperatures, we set the 15th of each month to the monthly average of nearshore water temperatures for Lake Ontario from 1989 to 2005 and interpolated (linear regression) between points to supply the remaining daily temperatures. Nearshore water temperatures were obtained by measuring the temperature of the water entering the Shoremount Municipal Water Treatment Plant, which is located near the midpoint of Lake Ontario on the south shore and draws water from a site 2.1 km from shore at a depth of about 14 m.

Chinook salmon diet was presumed to be 100% alewives because after their first summer in Lake Ontario, Chinook salmon eat mostly (>90%) alewives (Rand and Stewart 1998a; Lantry 2001) and because alewives were by far the most abundant prey fish in the lake during 1989–2005 (Owens et al. 2003; R.O., personal observation). We varied prey energy density annually based on observed variation in alewife K. Alewife K was determined each spring and fall from total lengths (mm) and weights (g) of alewives collected along the south shore via bottom trawls from late April to early May and in October (O'Gorman et al. 1997, 2008). Annual energy density of alewives was calculated from the mean of spring and fall K via the Madenjian et al. (2006) regression model relating energy density (Q; kJ/g) to K for large alewives (r^2, 0.75): $Q = -5.8073 + 15.6554K$.

Output from the bioenergetic model was the total annual consumption of an average-sized Chinook salmon from each age-group in each year. This output was then multiplied by the total abundance of Chinook salmon in a given age-group to yield total annual consumption by that age-group; overall annual consumption by the population was calculated as the sum of the age-group-specific consumption estimates. This method of calculating population consumption underestimates true consumption because it does not take into account the consumption by fish that died. To examine the magnitude of underestimation, we calculated the geometric mean abundance for hatchery fish age-groups 2–3 and 3–4 (square root of [$\log_{10}\text{CA}_{h,a} \times \log_{10}\text{CA}_{h,a-1}$]) and the percent change from the nominal estimate. The geometric mean provides an average annual value that takes into account the exponential decline in abundance, thus emulating the progressive loss of fish throughout the year. Because of the lack of survival estimates and initial numbers (i.e., abundance of age-0 fish) for wild-origin Chinook salmon, we were not able to use this approach for the entire population. Until further information becomes available, we do not believe that it is appropriate to assume that wild fish survival is the same as hatchery fish survival. Wild fish enter the lake substantially smaller than their hatchery-derived counterparts (Smith et al. 2006; Johnson 2008); thus, differences in size may lead to differing mortality. Along that line, Connerton et al. (2009) found that the proportion of wild fish increased with age in the 1992 and 1996 cohorts but decreased with age in the 2000 and 2002 cohorts, suggesting that there are differences in survival rates between the wild and hatchery fish and that the differences have changed over time.

Alewife biomass.—We compared total annual consumption by Chinook salmon to annual measures of alewife biomass in Lake Ontario. Although we only had measures of alewife density in U.S. waters, we assumed that density in Canadian and U.S. waters was similar; to arrive at the lakewide alewife biomass, we doubled the biomass estimate for U.S. waters because the amount of U.S. lake area is about half of the total lake area. Alewife biomass in U.S. waters during 1997–2005 was determined from area swept by bottom trawls, and biomass during 1989–1996 was determined by scaling a bottom trawl index of alewife biomass in U.S. waters (used to track alewife abundance since 1978; O'Gorman and Schneider 1986; O'Gorman et al. 2004) to alewife biomass in U.S. waters as determined from area swept by bottom trawls during 1997–2003. The 1997–2003 biomass index scaling was used because in 1997, use of more effective trawling gear for assessments was initiated and because the same depth range was fished during 1997–2003 as in all earlier years.

Alewives were assessed with bottom trawls in the U.S. waters of Lake Ontario by the U.S. Geological Survey (USGS) and the NYSDEC during late April to early May of each year (1989–2005, except 2001; see O'Gorman et al. [2004] for assessment method details). In general, trawls were fished in 12 areas spaced roughly 28 km apart in southern and eastern Lake Ontario from near the mouth of the Niagara River to the head of the St. Lawrence River. Range of depths fished was 8–150 m in 1989–2003 and 8–175 m in 2004–2005, when alewives occupied deeper water. Bottom trawls had cod ends of 9-mm (stretch measure) knotless nylon mesh and were towed at about 4.5 km/h during daytime along bottom contours for 10 min. The number of trawl tows made each year averaged 105 (range, 55 in 2002 to 122 in 1989 and 1991). Trawling gear used in 1997–2005 differed from that used in

1989–1996. The new trawl net opened higher than the old trawl net and caught more alewives at depths greater than 92 m. To account for the higher fishing power of the new trawling gear and the change in fishing power with depth, correction factors for abundance indices were applied to the 1997–2005 alewife catches to maintain continuity of the long-term index (O'Gorman et al. 2005). The possible need for a gear correction factor was also assessed from 73 paired tows made by two research vessels fishing side-by-side during 1995–1998. The two research vessels, one from the USGS and the other from the NYSDEC, had previously participated in side-by-side fishing trials with the trawling gear used in 1989–1996. These fishing trials found that there was no need for a correction factor to account for any potential difference in the fishing power of the two vessels, and thus we used the two vessels interchangeably when comparing trawling gear in 1995–1998.

Fish caught in each trawl tow were separated by species, counted, and weighed in bulk. When the total catch was large (>20 kg or so), we sorted, counted, and weighed a random subsample of 10–12 kg; the rest of the catch was weighed in aggregate, and composition was estimated by direct proportion. To estimate biomass of alewives in the U.S. waters of Lake Ontario during 1997–2005, we first divided the area into strata according to depth: 0–19, 20–39, 40–59, 60–79, 80–99, 100–119, 120–139, 140–159, and 160–179 m (the 160–179-m stratum was used in 2003–2005 only). The mean weight of alewives caught per hectare swept in each stratum was then multiplied by the total number of hectares in the stratum, and the sum of the products was the biomass in U.S. waters. Area swept was the product of the vessel speed over ground and the mean horizontal opening of the net in each depth stratum (measured by the NYSDEC with a wireless trawl monitoring system during assessments in 2004–2005). Because of logistical problems, only limited trawling was done in 2001, so alewife biomass in 2001 was estimated instead from bottom trawl catches during the early June assessment of rainbow smelt *Osmerus mordax* by using the relationship between area-swept estimates of alewife biomass in April and May and those in June during 1997–2000 and 2002–2006. The June rainbow smelt assessment is conducted in the same geographical area and across the same depth range as the April–May alewife assessment. The June estimates of alewife biomass, however, are always lower than those in April–May because of seasonal differences in the proximity of the fish to the bottom (O'Gorman and Schneider 1986). The index of alewife biomass for 1989–2005 was calculated in a similar manner except that (1) a fishing power correction (O'Gorman et al. 2005) was applied to catches in 1997–2005 to account for the change in trawling gear and (2) there was no adjustment for area swept in each stratum (i.e., mean weight of alewives caught per tow in each stratum was multiplied by the total number of hectares in the stratum).

Uncertainty.—The variables of greatest concern in estimating Chinook salmon abundance are the annual estimated percent hatchery fish in the stock and the age-specific survival rates. We systematically reran our abundance model, varying the hatchery fish percentage and survival rates individually; we then examined them collectively to determine the widest realistically possible bounds on our abundance estimates. First, we reran the model using the annual upper and lower 95% confidence limits of the annual proportions of wild and hatchery fish as estimated by Connerton et al. (2009). Second, we re-ran the abundance model by decreasing annual survival by 10% (i.e., $S - [S \times 10\%]$), and as a conservative test to provide the uppermost bound of potential consumption, we also increased survival by 10% (i.e., $S + [S \times 10\%]$). Finally, we explored the combined effects of variation in hatchery fish percentage and survival by varying both simultaneously. Because we were interested in the outermost bounds, we combined the two extremes: we first ran the model with both percent hatchery and survival at their higher bounds, producing the highest possible estimate of abundance; we then ran the model with both percent hatchery and survival at their lower bounds to produce the lowest possible estimate of abundance.

Results

Chinook Salmon Survival, Abundance, and Biomass

Hatchery fish survival was estimated to be 14.6% from stocking to age 1, 87.1% from ages 1 to 2, 54.0% from ages 2 to 3, and 3.0% from ages 3 to 4 (Appendix). We assumed no survival beyond age 4 (verified by aging done by Eckert [2007] and Bishop and Prindle [2007]). Empirically estimated total annual abundance of Chinook salmon in Lake Ontario was, on average, 1.83×10^6 individuals (interannual SD, 0.69×10^6 fish; nominal simulation including all age-groups except age-group 0–1) and ranged from 1.08×10^6 fish in 1997 and 2002 to 3.24×10^6 fish in 1992 (nominal simulation; Figures 3a, 4a). Based on observed age-group-specific mean weights, total Chinook salmon biomass ranged annually from 5.83×10^3 metric tons in 2002 to 23.04×10^3 metric tons in 1990 (mean, 11.33×10^3 metric tons; SD, 5.10×10^3 metric tons).

Through assessing uncertainty in key input variables (i.e., wild fish percentage, survival rates), we found that abundance was more sensitive to independent variation

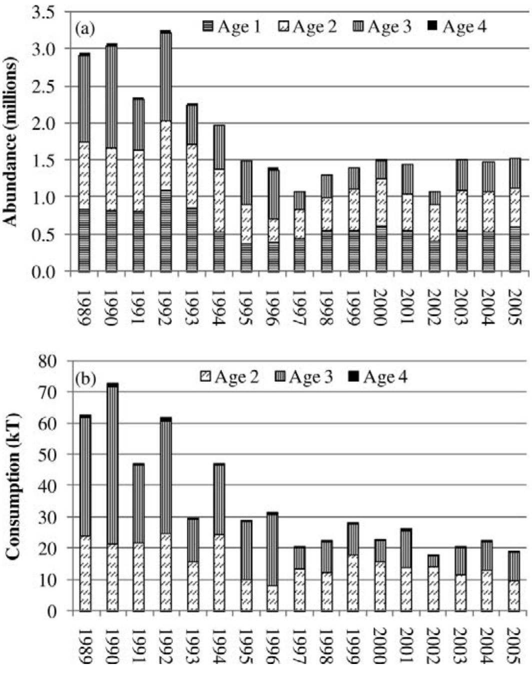

FIGURE 3.—Estimates (1989–2005) of Chinook salmon age-specific **(A)** abundance (× 10^6) for age-groups 1–4 and **(B)** prey consumption (× 10^3 metric tons) for age-groups 2–4 derived from the nominal simulation (see Methods). Consumption was not modeled for age-group 0–1.

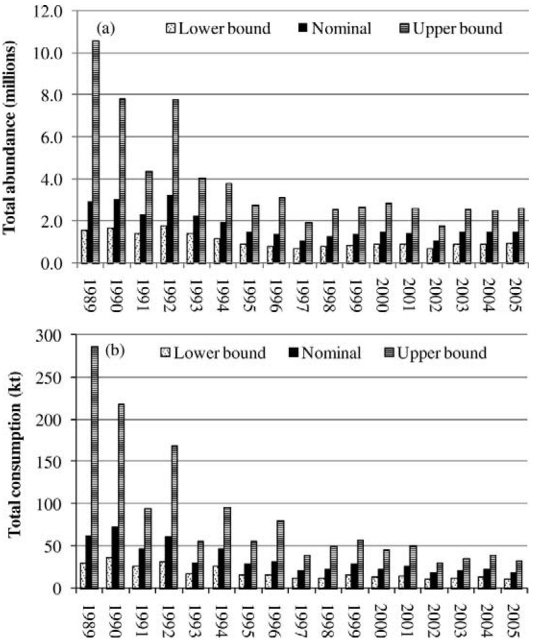

FIGURE 4.—Nominal (see Methods) 1989–2005 estimates of Chinook salmon lakewide total **(A)** abundance (× 10^6) and **(B)** prey consumption (× 10^3 metric tons) (all age-groups combined) in Lake Ontario, compared with the upper and lower bound simulation results (upper = upper 95% confidence limit [CL] of the wild fish percentage in the population and a 10% increase in survival; lower = lower 95% CL of the wild fish percentage and a 10% decrease in survival).

in the annual age-specific percentage of naturally produced fish (percent wild) than to 10% variation in survival rates (Table 1; Figure 4a). Increasing the proportion of wild fish had a larger influence on the results than a decrease, whereas the opposite was true for changes in annual survival rates and changes in both variables. Further, due to the additive effects of the variable alterations, older age-groups showed greater percent change than younger age-groups for increases and decreases in both the percentage of wild fish and survival rates (Table 1). Combining the uncertainty associated with both variables (i.e., using the upper 95% confidence limit [CL] for the wild fish percentage and using a 10% increase in age-specific survival rates) increased the estimated abundance (pooled across age-groups) by 53.3% on average relative to the nominal simulation, whereas the combination of the two lower extremes resulted in, on average, a 68.7% decrease from the nominal simulation (Table 1).

Chinook Salmon Consumption Versus Alewife Biomass

Based on annual observed mass at age, overall gross conversion efficiency (GCE; pooled across age-groups 1–4 and all years) was 15.8% in the nominal simulation, although as expected there were substantial age-specific differences. On average, GCE decreased by about 50% annually as fish aged (Table 2). Even though the mean GCE of the oldest and largest fish (age-group 3–4) was less than a quarter of the GCE for the youngest group

TABLE 1.—Percent change in mean annual age-group-specific abundance and total abundance (last row; age-groups pooled) of Lake Ontario Chinook salmon from nominal (*N*) results as effected by changes in the key input variables of estimated wild fish percentage (*W*; Connerton et al. 2009) and survival rate (*S*). The 95% confidence intervals around values of *W* reported by Connerton et al. (2009) were used for the upper bound (*U*) and lower bound (*L*); 10% of each *S* estimate was added to (*U*) or subtracted from (*L*) the nominal *S* estimates.

Age-group	S_N, W_U	S_N, W_L	S_U, W_N	S_L, W_N	S_U, W_U	S_L, W_L
1	34.3	−32.3	9.1	−11.1	40.3	−47.0
2	35.7	−35.5	17.4	−23.5	46.9	−67.2
3	54.1	−46.5	24.9	−37.2	65.5	−100.9
4	54.5	−46.7	31.7	−52.4	68.9	−123.6
Total	42.7	−37.7	17.6	−22.9	53.3	−68.7

TABLE 2.—Means and ranges for estimated age-group-specific abundance in September, average individual gross conversion efficiency (GCE), proportion of maximum consumption ($p[C_{\max}]$ value from bioenergetics model), and prey consumption for Lake Ontario Chinook salmon, 1989–2005, under the nominal simulation (standard parameters).

Age-group	Abundance ($\times 10^3$) mean (range)	GCE mean (range)	$P(C_{\max})$ mean (range)	Prey consumption ($\times 10^3$ metric tons) mean (range)
0–1	611 (366–1,084)	—	—	—
1–2	630 (317–936)	0.18 (0.16–0.22)	0.83 (0.69–1.04)	15.82 (8.09–24.54)
2–3	566 (177–1,368)	0.11 (0.07–0.15)	0.61 (0.47–0.82)	17.88 (3.93–50.46)
3–4	18 (6–39)	0.04 (0.00–0.09)	0.41 (0.25–0.72)	0.44 (0.09–0.93)

modeled (age-group 1–2), the sharp decline in abundance of age-3–4 fish in most years resulted in their estimated total consumption being two orders of magnitude lower than those of the younger age-groups (Table 2; Figure 3b). Overall, because mortality is annual rather than daily, our nominal consumption estimates almost certainly underestimate total consumption. This is especially true in the older age-groups, where the sharp decline in abundance resulted from open-lake harvest occurring largely between April and September (55–60%) and from spawning losses in October and November (40–45%; Appendix). Nominal abundance estimates were lower than the annual geometric mean abundance of hatchery-origin Chinook salmon (initial $\mathrm{CA}_{h,t-1,a-1}$ and final $\mathrm{CA}_{h,t,a}$, which approximates evenly distributed daily mortality) by 62% for age-group 1 (stocking to September age 1), 8% for age-group 2, 28% for age-group 3, and 83% for age-group 4. However, because of the lack of information regarding the survival and initial abundances of wild-origin Chinook salmon in Lake Ontario, we were unable to use this approach for the entire population.

Notwithstanding the potentially large underestimation, 17-year mean annual total consumption by Chinook salmon (ages 1–4 pooled) was 34.14×10^3 metric tons (SD, 17.28×10^3 metric tons) for the nominal simulation and ranged between a low of 17.93×10^3 metric tons in 2002 and a high of 72.59×10^3 metric tons in 1990 (Figure 4b). The average estimated consumption upper bound (age-groups 1–4 pooled, all years; using the upper 95% CL for the wild fish percentage and a 10% increase in survival) was 85.35×10^3 metric tons (SD, 72.71×10^3 metric tons), whereas the lower bound (using the lower 95% CL for the wild fish percentage and a 10% decrease in survival) was 18.49×10^3 metric tons (SD, 8.09×10^3 metric tons; Figure 4b).

Average annual total lakewide alewife biomass (pooled across ages) from 1989 to 2005 was 173.7×10^3 metric tons and ranged from 62.4×10^3 metric tons in 1998 to 345.5×10^3 metric tons in 1989; the vast majority of biomass was composed of adult alewives (Figure 5a). Alewife energy density averaged 4.83 kJ/g during the study but increased steadily from a low of 4.13 kJ/g in 1992 to a high of 5.86 kJ/g in 2005 (Figure 6). For the nominal simulation (pooled across age-groups 1–4 and across all years), the estimated Chinook salmon population consumed 22% of the estimated alewife biomass, with annual values ranging from 11% in 1994 to 44% in 1990 (Figure 5b). For the upper bound (using the upper 95% CL of the wild fish percentage and a 10% increase in survival), the estimated Chinook salmon population (pooled across age-groups 1–4 and all years) consumed, on average, 51% of the estimated alewife biomass (Figure 5b); for the lower bound (using the lower 95% CL for the wild fish percentage and a 10% decrease in survival), the average was 12%.

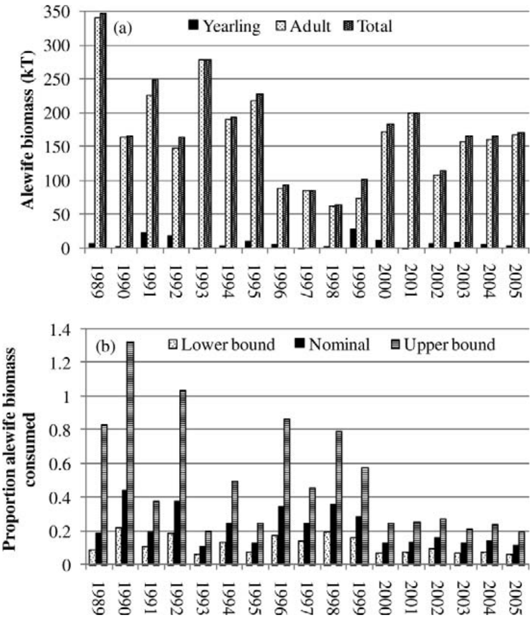

FIGURE 5.—Estimated annual (1989–2005) lakewide **(A)** alewife biomass ($\times 10^3$ metric tons; age 0, adults, and total) in Lake Ontario and **(B)** proportion of the total alewife biomass consumed by Chinook salmon under the nominal simulation and upper and lower bound simulations (defined in Figure 4).

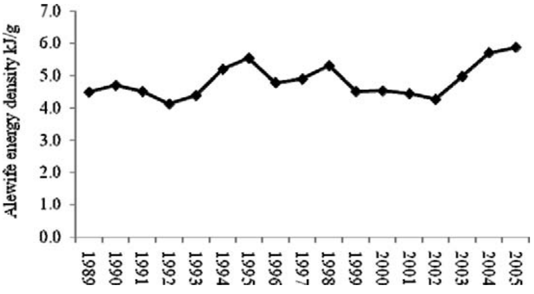

FIGURE 6.—Estimated mean annual energy density (kJ/g, wet weight) of alewives in Lake Ontario.

Comparisons of Past and Present Estimates

Our estimates of alewife biomass density in Lake Ontario (1989–2005) ranged from 33 kg/ha in 1998 to 183 kg/ha in 1989 (average, 91.97 kg/ha; Table 3). Our year-specific estimates of alewife density are very close to previous estimates for Lake Ontario except the fall 1990 estimate reported by Mason et al. (2001); this discrepancy may be related to differences in sampling season. Relative to Lakes Michigan and Huron, however, the biomass density of alewives in Lake Ontario in recent years (e.g., 2002–2006) is an order of magnitude higher (Table 3).

We estimated mean Chinook salmon biomass density to be 6.0 kg/ha in Lake Ontario between 1989 and 2005 (range, 3.1 kg/ha in 2002 to 12.2 kg/ha in 1990; Table 3). Previous estimates include results from a population model in 1990 (excluding wild fish; Rand and Stewart 1998b) and hydroacoustic estimates in 1991 and 1992 (Goyke and Brandt 1993). Not surprisingly, our estimates for 1990 are more than five times higher than the Rand and Stewart (1998b) estimate, which excluded wild fish. However, our (fall) 1991 estimate was about a third of Goyke and Brandt's (1993) fall estimate, though the 1992 estimates were very similar. Available estimates for salmonids in Lake Michigan are highly variable; 1987 estimates based on size-spectra analysis were an order of magnitude lower than estimates for the same year based on population modeling (Sprules et al. 1991). Our long-term average, which does not include 1987, is more consistent with the size-spectra estimates (Table 3).

Our estimated ratio of alewife : Chinook salmon biomass (kg) was, on average, 16.5 kg of alewives for each 1 kg of Chinook salmon (range, 7.2:1.0 in 1990 to 27.4:1.0 in 1993; Table 3). Our 1991 estimate is approximately 2–4 times that of Goyke and Brandt (1993) but reasonably consistent with their 1992 estimate. For reference, Sprules et al. (1991) estimated the planktivore : piscivore ratio in 1987 to be 32:1 via a size-spectra approach but between approximately 2:1 and 4:1 via a population modeling approach (Table 3).

Surprisingly, our 1990 estimate of total Chinook salmon abundance is strikingly similar to that of Rand and Stewart (1998b; Table 4); however, dramatic age-specific differences were evident. Further, Rand and Stewart (1998b) did not have sufficient data to include wild recruited fish; therefore, their estimate was based strictly on hatchery production. In contrast, wild fish contributed over half of the total abundance of Chinook salmon in our estimate, and accordingly our age-specific estimates of hatchery fish abundance are substantially lower than Rand and Stewart's (1998b) estimates for ages 1–3 (but we estimated more age-4 hatchery fish than they did). Our estimated GCEs were 14% lower for age 2 and 67% lower for age 4 relative to those reported by Rand and Stewart (1998b). Differences in GCE were at least partially responsible for our consumption estimates being well over three times greater than theirs even though we were unable to include age-1 consumption (i.e., from age-group 0–1). Differences in consumption were evident for all ages but were greatest for ages 3 and 4 (Table 4).

Discussion

Chinook Salmon Consumption Versus Alewife Biomass

Based on our updated and revised lakewide estimates of Chinook salmon abundance, biomass, and consumption in Lake Ontario, in conjunction with our revised estimates of lakewide alewife biomass, we agree with the conclusions of numerous other authors that salmonine predation pressure in some years may indeed be pushing the limits of prey fish sustainability (e.g., Stewart et al. 1981; Kitchell and Crowder 1986; Brandt et al. 1991; Stewart and Ibarra 1991; Jones et al. 1993; Rand et al. 1994; Rand and Stewart 1998a, 1998b). Our nominal calculations excluding Chinook salmon under 16 months of lake age indicated that, on average, the Chinook salmon population in Lake Ontario consumed 22% of the alewife biomass each year between 1989 and 2005 (maximum observed value was 44% in 1990). Comparing Chinook salmon consumption with total alewife production would provide a better assessment of prey demand; however, the only estimates of Lake Ontario alewife production (P; 281.2×10^3 metric tons/year; Rand and Stewart 1998b) and biomass (B; 186.05×10^3 metric tons; Rand et al. 1995) were for 1990–1991; those data allowed us to calculate a single-year P/B value of 1.51 (similar to the 1.56 derived from Brandt et al. [1991] for alewives in Lake Michigan in 1987). Based on this rough conversion, annual alewife production in Lake Ontario was 51% higher than the estimated spring biomass. Again excluding fish under 16 months of lake age, Chinook salmon consumed, on

TABLE 3.—Predator and prey biomass density (BD; kg/ha) estimates for Lakes Ontario, Michigan, and Huron.

Species	Lake	Year(s)	Mean BD (kg/ha)	BD range, kg/ha (year)	Source
			Prey fish		
Alewife	Ontario	1989–2005	91.97	33.0 (1998)–183.0 (1989)	This study
All pelagic planktivores	Ontario	Fall 1990	191		Mason et al. 2001
		Spring 1992	96		
Pelagic prey	Ontario	Summer 1991	119.5		Goyke and Brandt 1993
		Fall 1991	147.1		
		Spring 1992	68.2		
Alewife	Ontario	Spring 1990	87.3		This study
		Spring 1991	131.57		
		Spring 1992	86.6		
All pelagic planktivores	Michigan	1987	61	94–137[b]	Sprules et al. 1991
Alewife	Michigan	2002–2004	9.1		Madenjian et al. 2006
All pelagic planktivores	Huron	2004–2006		2–7[d]	Schaeffer et al. 2008
Alewife	Ontario	2002–2004[e]	78	60–87	This study
		2004–2006[e]	69	31–90	
			Predators		
Chinook salmon	Ontario	1989–2005	6.0[a]	3.1 (2002)–12.2 (1990)	This study
Chinook salmon	Ontario	1990	2.33		Rand and Stewart 1998
Chinook salmon	Ontario	Summer 1991	14.9		Goyke and Brandt 1993
		Fall 1991	29.7		
		Spring 1992	9.8		
Chinook salmon	Ontario	1990	12.2[a]		This study
		1991	8.0[a]		
		1992	10.4[a]		
All salmonids	Michigan	1987	1.9[c]	34–56[b]	Sprules et al. 1991
			Prey : predator		
Alewife : Chinook salmon	Ontario	1989–2005	16.5[a]	7.2 (1990)–27.4 (1993)[a]	This study
Prey : predator	Ontario	Summer 1991	8.02	—	Goyke and Brandt 1993
		Fall 1991	4.95	—	
		Spring 1992	6.96	—	
Alewife : Chinook salmon	Ontario	1991	16.5[a]	—	This study
		1992	8.35[a]	—	
Planktivores : piscivores	Michigan	1987	32.1[c]	1.7–4.0[b]	

[a] Estimates do not include age-0 Chinook salmon.
[b] Estimates derived from population models (independent of biomass size-spectra [BSS] estimates).
[c] Estimates predicted from BSS analysis.
[d] Approximate values from Figure 4b in Schaeffer et al. (2008).
[e] Value presented as mean over range of years.

average (1989–2005), 14% of the total alewife production in the nominal estimates (range, 7–29%; using a *P*/*B* conversion of 1.51 for all years). This consumption level might appear reasonably sustainable except that the Chinook salmon is only one of several piscivores that utilize alewives as a primary prey item (Lantry 2001). Furthermore, consumption by Chinook salmon alone exceeded the 10% of production sustainable yield level suggested by Downing and Plante (1993) in 10 of the 17 years examined.

TABLE 4.—Comparison of Chinook salmon abundance, total prey consumption (*C*), and gross conversion efficiency (GCE) during 1990 in Lake Ontario between estimates of Rand and Stewart (R&S; 1998b) and this study. The data for our study correspond to the year leading up to the specific age (e.g., there were 8.42×10^6 age-2 fish in September 1990 that had a GCE of 19% and consumed 21.21×10^3 metric tons of prey in the previous year (age 1 to 2; September 1989 to September 1990).

	Abundance ($\times 10^3$)		GCE		Total *C* ($\times 10^3$ metric tons)	
Age	R&S 1998b	This study Total (hatchery; wild)	R&S 1998b	This study	R&S 1998b	This study
1	1,731	818 (481; 337)	0.29	—	4.46	—
2	911	842 (428; 414)	0.22	0.19	11.20	21.21
3	374	1,368 (249; 1,119)	0.12	0.12	5.18	50.46
4	5	39 (7; 32)	0.12	0.04	0.08	0.93
Combined	3,021	3,067 (1,165; 1,902)			20.92	72.60

In addition, the cumulative effects of this level of predation over several years has probably contributed to reducing alewife numbers, especially when alewife reproduction has been insufficient to replace the population losses from salmonine predation. A few strong alewife year-classes (e.g., 1990, 1991, 1998; Figure 5a) helped maintain the population for a few consecutive years, but during periods with successive small year-classes (e.g., 1992–1997, 2000–2004), the adult alewife population declined, with obvious effects on Chinook salmon growth (Bishop and Prindle 2007). Chinook salmon are known (Lantry 2001) to focus their diet on adult alewives (over 69% adults and approximately 30% yearlings in 1999), especially in years with low alewife yearling abundance (e.g., 95% adults in summer 1998). Therefore, predation losses from the adult alewife population are compounded after successive years of low yearling recruitment, and the population's sustainability can eventually rest on one strong year-class. The system then depends on the chance that sufficient numbers of adults will remain to produce another strong year-class when environmental conditions are favorable (i.e., warm water temperatures during May–July and a short winter; O'Gorman et al. 2004).

Moreover, our results very likely underrepresent the risk of prey fish overexploitation. Simulations based on realistic upper extreme values of two fundamentally important model inputs—the annual percentage of wild fish (equation 2) and age-group-specific survival rates of hatchery fish (equation 3)—increased the mean annual percentage of alewife biomass consumed to 51%. Total consumption exceeded 100% in 2 of the 17 years and was over 40% in 8 of the 17 years. Our analysis also did not account for consumption by age-0 Chinook salmon, and most importantly, Chinook salmon are only one species of a far larger salmonine assemblage (e.g., coho salmon *Oncorhynchus kisutch*, steelhead *Oncorhynchus mykiss*, brown trout *Salmo trutta*, Atlantic salmon *Salmo salar*, and lake trout *Salvelinus namaycush*) that also rely on alewives as a major prey source (Lantry 2001).

Younger Chinook salmon were excluded from our model because of our focus on consumption of those alewife life stages for which we have data (i.e., yearling and older alewife abundance; Figure 5a; Bishop and Prindle 2007). Chinook salmon in age-group 0–1 probably switch to piscivory by the fall of their first year of life and are certainly gape-limited to consuming only age-0 alewives (mostly <9 cm long at that time). By spring, when the alewife survey is conducted, age-1 Chinook salmon are approximately 45 cm long and have begun to include larger alewives in their diet. Our simulation did not estimate consumption by age-1 fish until September (about 16 months of lake-age because our calculations begin in September at age 1). New York State and the province of Ontario stock approximately 2.6×10^6 age-0 Chinook salmon annually into Lake Ontario and its tributaries, and in 2005 over 5×10^6 Chinook salmon were produced by natural spawning in the Salmon River alone (Everitt 2006). There is evidence of extensive natural reproduction in other New York and Ontario tributaries as well (M.J.C., unpublished data; I. Crane and M. Gross, University of Toronto, personal communication). Failure to include these younger fish probably underestimates actual Chinook salmon consumption and may have additional negative influence on the recruitment of alewives. O'Gorman et al. (2004) concluded that predation influenced the survival of juvenile alewives in Lake Ontario from 1978 to 2000.

We are most confident in our estimate of age-3 Chinook salmon abundance because we had the most data for that age-group throughout the study period; estimates of abundance at younger ages are probably underestimates because cohort abundance occasionally increased through ontogeny. Although this phenomenon is biologically impossible, it is due mathematically to higher age-specific estimates of the proportion of wild fish for ages 3 and 4 than for the younger fish, resulting in an increase in estimated wild fish through ontogeny. Our total abundance estimates (hatchery + wild fish; equations 1 and 2) are based upon the number of hatchery fish surviving from stocking to each successive age, which neatly follows an expected decline based on the age-specific survival rates (e.g., Table 1). In contrast, the number of wild fish is calculated simply as the product of the number of hatchery fish and the age-specific proportion of wild fish (equation 2), such that even though the number of hatchery fish declines through ontogeny, as it should, the number of wild fish often increases through ontogeny based on the higher observed proportion of wild fish in the open-lake mixed stock (Connerton et al. 2009). Possible reasons for the observed increase in the proportion of wild fish may include later age at maturity, later emigration to the offshore habitat, smaller size at age and therefore lower recruitment to angling gear at younger ages, and differential habitat use. All of these factors have the potential to bias estimates of the wild proportion for younger fish because of undersampling.

Future Research Needs

There are several factors that require additional information to improve the current estimates of Chinook salmon consumption in Lake Ontario and to develop a lakewide, ecosystem-level predator–prey model. First, a comprehensive inventory of wild smolt production throughout the entire basin and an understanding of the factors that drive wild fish survival and recruitment would aid in making more accurate estimates of wild fish abundance and survival. Currently, estimates of smolt production exist only for the Salmon River and only for recent years (Everitt 2006)—years for which estimates of the proportion of wild adults do not yet exist. However, if we assume that the level of natural production observed by Everitt (2006) is temporally consistent, it is clear that survival of wild smolts to older ages is poor (e.g., over 5×10^6 smolts produced in 2005 compared with an average of 300,000 wild age-1 fish in the lakewide population during 1989–2005). It is possible that this enormous surplus of Chinook salmon production may in fact help feed the adult salmonid community and buffer the alewife population from overpredation. Alternatively, during years when alewives are abundant, they may reduce cannibalism on young salmonids, increasing their survival (Johnson et al. 2007). Published data supporting the cannibalism hypothesis are lacking. However, Lantry and Stewart (2000) found that if each yearling rainbow smelt ate a single young-of-the-year rainbow smelt in each year, there would be substantial population-level consequences. Elrod et al. (1995) found that cannibalism was an important factor for the survival of stocked lake trout yearlings in Lake Ontario. Thus, cannibalism may help to stabilize both predator and prey population dynamics but still occurs at such low frequencies that it is difficult to detect in a typical diet survey.

These estimates, as well as future modeling and management efforts, would also be aided by a longer time series of hatchery fish survival estimates. Here, we derived survival estimates for only four cohorts and used fixed age-group-specific survival rates throughout the entire time series, where clearly we might expect some interannual variation. The estimates presented here were less sensitive to variation (10% increase or decrease) in survival rates than to variation in the annual proportion of wild fish (Table 2). As for the wild fish, a comprehensive understanding of how population characteristics, body size, food web, and ecosystem variations affect their annual survival rates, as well as those of hatchery-derived Chinook salmon, would also be instrumental to future modeling efforts. Fortunately, Ontario Ministry of Natural Resources and NYSDEC implemented a mass-marking program on Lake Ontario in 2008 in which all hatchery fish are now clipped, and stocked Salmon River fish are tagged by an automated mass-marking system. Results from these studies and the larger systemwide Great Lakes mass-marking initiative will go a long way towards increasing our understanding of the hatchery and wild Chinook salmon populations.

Comparisons of Past and Present Estimates

Overall, our alewife biomass density estimates are largely consistent with previous year-specific estimates (Goyke and Brandt 1993; Mason et al. 2001), 1990 being an exception that is possibly related to differences in sampling season. Mason et al. (2001) estimated Lake Ontario alewife biomass density to be 191 kg/ha in the fall of 1990, whereas in spring 1990 we estimated a biomass density of 87 kg/ha. Recruitment of new individuals and growth of existing individuals between spring and fall may, at least in part, contribute to this large difference. Data from Goyke and Brandt (1993) support this contention; they estimated a 23% increase in alewife biomass density in Lake Ontario between summer 1991 and fall 1991 (Table 3). Additionally, previous estimates (Goyke and Brandt 1993; Mason et al. 2001) included all pelagic prey fish, whereas ours were exclusive to alewives. Rainbow smelt are the only other pelagic prey fish that would add substantially to our estimates, and it is likely that they account for some of the remaining difference between our estimates and earlier ones. Compared with Lakes Michigan and Huron (Madenjian et al. 2006; Schaeffer et al. 2008), alewife biomass density in Lake Ontario has been an order of magnitude greater in recent years (2002–2006), and this has consistently been the case for the last two decades (O'Gorman and Schneider 1986).

Our estimates of Chinook salmon biomass density are less consistent with previous studies than our alewife data. For summer and fall 1991 in Lake Ontario, Goyke and Brandt (1993) reported estimates that were nearly two to four times greater than our estimate for 1991; however, estimates for 1992 from both studies were very similar. The Goyke and Brandt (1993) study was conducted in spring; thus, given recruitment and growth, we would expect their estimate to increase by fall. Detailed comparisons between our work and that of Rand and Stewart (1998b) should be considered tentative at best. Rand and Stewart's (1998b) estimates were based on population models that ran from annulus to annulus (May–May, with the final spawning age-class from May to October), whereas due to available data, our empirical calculations ran from September to September. Further, due to insufficient empirical data at the time, Rand and Stewart (1998b) did not include consideration of wild fish or nonharvest spawning mortality. We were able to capitalize on new information on the relative abundance of wild fish (i.e., proportion of stock; Connerton et al. 2009) and nonharvest spawning mortality (Everitt

2006) to refine survival rates. Inclusion of these two factors resulted in lower survival rates than previously used by Rand and Stewart (1998b). Because Rand and Stewart's (1998b) work was based on the assumption of limited or no wild fish recruitment, our estimates of strictly hatchery fish abundance should be more directly comparable. The large discrepancies (i.e., present estimates of hatchery-derived fish are far lower) between the age-specific estimates demonstrate the effect of the revised survival rates. Nonetheless, overall abundance estimates from both studies for 1990 were surprisingly similar, although age-specific estimates differed rather substantially. As discussed above, however, our estimates are probably low and therefore, as we would expect, are probably higher in reality than Rand and Stewart's (1998b) estimates. It is also possible that without knowledge of wild reproduction, the survival estimates and initial population values reported by Rand and Stewart (1998b) may have inadvertently included wild fish, leading to the surprising similarity in our overall abundance estimates.

There were differences in Chinook salmon GCE and consumption between the Rand and Stewart (1998b) estimates and ours. These differences were probably strongly influenced by (1) our use of a warmer thermal regime (Wurster et al. 2005) than that used by Rand and Stewart (1998b) and (2) potentially differing initial body mass assumptions. Rerunning our bioenergetics model using an annual thermal profile similar to that used by Rand and Stewart (1998b; maximum summer temperature of 11°C) increased the observed GCE for age-group 4 by 27% and lowered consumption by 32%. Another factor that may have contributed to GCE differences in age-group 4 between our study and Rand and Stewart's (1998b) study was our use of mean weight at age in September and therein not taking into account the loss of the largest fish of each age-group to spawning in the subsequent months. To examine this effect, we decreased the initial mass of age-4 Chinook salmon by 15%, which resulted in a 55% increase in GCE and a 19.6% increase in consumption over the nominal estimate. Overall, when we altered our assumptions of the temperature occupied by Chinook salmon and their mean weight at age to more closely emulate those conditions modeled by Rand and Stewart (1998b), our estimates of GCE and consumption were more closely aligned to theirs.

In conclusion, we estimate that between 1989 and 2005, Lake Ontario has supported, on average, 11.33×10^3 metric tons of Chinook salmon, or 1.83×10^6 individuals between the ages of 1 and 4. For the same 17-year period, we provide new lakewide alewife biomass estimates that were, on average, 174×10^3 metric tons annually. As a conservative estimate, Chinook salmon consume, on average, the equivalent of 22% of the alewife biomass annually, with realistic values approaching 45% (nominal simulation) and upper estimates exceeding 100% (in an individual year under the upper bound simulation scenario with increased age-specific survival and wild fish percentage). Because Chinook salmon are only one species of a much larger multispecies assemblage of salmonines that rely on alewives as a major food source, we certainly agree with past researchers and managers that the system may be operating at or near carrying capacity. Recent declines in Chinook salmon size at age are consistent with this conclusion (Bishop and Prindle 2007; Eckert 2007).

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Appendix: Calculation of Age-Specific Survival Rates for Hatchery Chinook Salmon

The number of fish stocked annually in the Salmon River and throughout Lake Ontario were obtained from NYSDEC reports (Eckert and Connerton 2007); the ratio provided a "lake factor" (i.e., number stocked in the Salmon River divided by the number stocked lakewide), which represents the proportion of total lakewide stocked fish of Salmon River origin (Table A.1). To obtain age-specific open-lake harvest losses of

TABLE A.1.—Total number of age-0 Chinook salmon stocked throughout Lake Ontario (U.S. and Canadian waters) and specifically at the mouth of the Salmon River, New York (Eckert and Connerton 2007); the lake factor is the proportion of fish stocked in the Salmon River.

Year-class	Total number stocked	Salmon River number stocked	Lake factor
2000	1,906,543	360,000	0.19
2001	1,893,686	341,800	0.18
2002	1,908,002	342,500	0.18
2003	1,700,374	346,000	0.20
2004	1,962,565	360,000	0.18

TABLE A.2.—Age (% composition) and origin (% hatchery) of Lake Ontario Chinook salmon harvested from the open lake in U.S. or Canadian waters during 2004 and 2005; data are from Eckert (2007) and J. Bowlby (Ontario Ministry of Natural Resources, unpublished data). The percentage of hatchery-origin fish was derived from Connerton et al. (2009).

Age	Cohort	U.S. waters	Canada waters	Percent hatchery
		Year: 2004		
1	2003	6.70	23.76	65.4
2	2002	57.10	31.11	57.2
3	2001	35.40	45.14	37.9
4	2000	0.70	0.00	37.9
Combined (number of fish)		51,443	18,182	
		Year: 2005		
1	2004	3.50	20.98	65.4
2	2003	31.60	19.07	57.2
3	2002	64.10	58.04	37.9
4	2001	0.70	1.36	37.9
Combined (number of fish)		68,957	20,731	

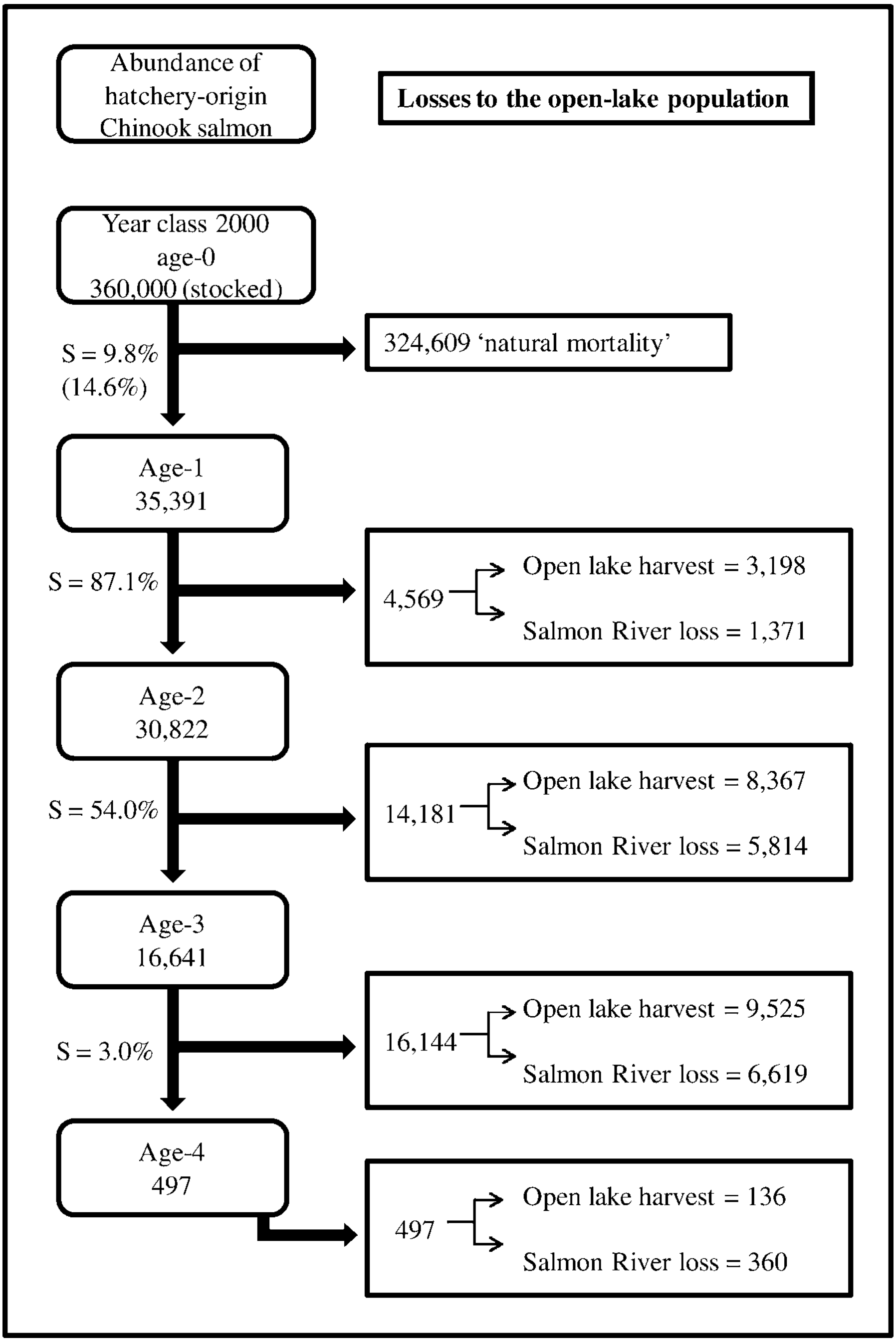

FIGURE A.1.—Flow diagram of the 2000 year-class of hatchery-stocked Chinook salmon as an example of when and how mortality occurred (numbers are abundances and percentages are survival rates *S*); we used this information in calculating *S* (the *S* for age 0–1 is for this specific case, and the mean value is below it in parentheses; Table A.6).

TABLE A.3.—Total (including all ages) loss of Lake Ontario Chinook salmon from the open-lake population into the Salmon River, New York, during the spawning migrations in 2004 and 2005, as effected by angler harvest, hatchery harvest, and in-stream mortality based on carcass count estimates (Everitt 2006; Prindle and Bishop 2007).

Year	Carcass estimates	Angler harvest	Hatchery harvest	Total Salmon River loss
2004	13,022	24,360	10,149	47,531
2005	27,748	25,988	8,132	61,868

TABLE A.4.—Age (% composition) and origin (% hatchery) of Lake Ontario Chinook salmon in the Salmon River, New York, in 2004 and 2005 (Bishop and Prindle 2007; Connerton et al. 2009). We assumed that the percent age composition of hatchery fish leaving the open lake for spawning was the same as that of the open-lake population.

Age	2004 (%)	2005 (%)	Percent hatchery
1	7.00	2.00	65.4
2	52.00	22.00	57.2
3	39.00	75.00	37.9
4	2.00	1.00	37.9

TABLE A.5.—Total annual age-specific losses of Lake Ontario Chinook salmon from the open-lake population, including open-lake harvest and spawning losses but not including other (natural) mortality. Age-specific Salmon River, New York, loss was calculated as the product of total Salmon River loss (Table A.3), proportion age composition, and proportion of hatchery-origin fish (Table A.4). The overall age-specific, open-lake harvest was calculated as total U.S. harvest multiplied by U.S. age composition and hatchery proportion plus the total Canadian harvest multiplied by Canadian age composition and hatchery proportion (all from Table A.2). Total age-specific loss is the sum of Salmon River and open-lake losses.

Year sampled	Age	Year-class	Salmon River loss	Open-lake harvest (U.S. + Canada)	Total age-specific loss
2004	1	2003	2,175	5,077	7,252
	2	2002	14,135	20,034	34,169
	3	2001	7,026	10,013	17,038
	4	2000	360	137	497
2005	1	2004	809	4,421	5,230
	2	2003	7,784	14,723	22,507
	3	2002	17,586	21,313	38,899
	4	2001	235	290	524

fish stocked in the Salmon River, the total open-lake catch (U.S. + Canadian; Table A.2) of Salmon River origin (total catch × lake factor) was multiplied by age-specific catch frequencies (data from creel survey reports by Eckert [2007] and J. Bowlby [Ontario Ministry of Natural Resources, unpublished data]) and age-specific wild proportion estimates (Connerton et al. 2009; Table A.2). Total Salmon River losses were the sum of the age-specific angler-harvest estimates from a tributary creel survey conducted in 2006 (Prindle and Bishop 2007), hatchery harvest estimates based on counts in the hatchery (Bishop and Prindle 2007), and total Chinook salmon carcasses estimated by a carcass survey within the river (Everitt 2006; Table A.3). Age-specific losses from the Salmon River were also multiplied by the hatchery percentage to isolate fish of hatchery origin (Table A.4). The sum of all Salmon River losses and open-lake losses represented the number of fish dying by age and cohort (Table A.5).

Setting up a matrix containing total losses (mortality), with year-class on the vertical and age on the horizontal, allowed us to estimate missing cells using proportions formed by adjacent and opposite cells (Table A.6). This procedure assumes that the number of fish dying is proportional among ages and years. The population abundance (number of fish remaining) of each age-group within a given year-class was estimated by summing the total number of fish dying for that age and all subsequent ages within the cohort. Survival was then calculated as the abundance of age a in a given year t divided by the abundance of previous age-group $a-1$ in the previous year $t-1$ (Table A.6).

Mean age-specific survival was used in all further modeling efforts unless otherwise indicated (e.g., for abundance estimate bounds, we used $S \pm [S \times 10\%]$). This version of the model has similar assumptions to those of Rand and Stewart (1998) except that we additionally take into account wild-origin fish and, in doing so, we assume that wild and hatchery spawners return (mostly in October) in proportion to their estimated occurrence in the open lake during September—an assumption that is supported by observed data (M.J.C., unpublished data).

TABLE A.6.—Three-step calculation of mortality and survival of Lake Ontario Chinook salmon by age-group and year-class (YC; 2000–2004). In step 1, the number of fish dying was computed directly from Table A.5 (bold italic font) or by forming proportions with adjacent and opposite cells (e.g., the number of age-1 fish [i.e., age-group 0–1, etc.] dying from the 2002 YC [11,010 fish] was estimated by forming a proportion between the number of age-1 and age-2 fish dying from the 2003 YC [7,252/22,507] and then multiplying by the number of age-2 fish dying from the 2002 YC [34,169]). In step 2, the estimated abundance was derived by summing the total number of fish dying for that age and all subsequent ages within the cohort (e.g., the abundance of age-1 fish from the 2000 YC was the total of all fish that died at age 1 and beyond because they had to have been alive at age 1 to die at a subsequent age; i.e., $35{,}391 = 4{,}569 + 14{,}181 + 16{,}144 + 497$. In step 3, mortality ($M$) and survival ($S$) were calculated as abundance of age a in a given year t divided by abundance of the previous age-group $a - 1$ in the previous year $t - 1$.

YC	Stock	Age 0–1	Age 1–2	Age 2–3	Age 3–4
Step 1: number of fish dying					
2000	360,000	4,569	14,181	16,144	***497***
2001	341,800	4,822	14,967	***17,038***	***524***
2002	342,500	11,010	***34,169***	***38,899***	1,197
2003	346,000	***7,252***	***22,507***	25,622	788
2004	360,000	***5,230***	16,231	18,477	569
Step 2: estimated abundance remaining					
2000		35,391	30,822	16,641	497
2001		37,351	32,529	17,562	524
2002		85,274	74,265	40,096	1,197
2003		56,170	48,918	26,411	788
2004		40,506	35,276	19,046	569
Step 3: mortality					
2000		0.902	0.129	0.460	0.970
2001		0.891	0.129	0.460	0.970
2002		0.751	0.129	0.460	0.970
2003		0.838	0.129	0.460	0.970
2004		0.887	0.129	0.460	0.970
Mean M		0.854	0.129	0.460	0.970
$S(=1 - M)$		0.146	0.871	0.540	0.030