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# Length Frequency Age Estimations of American Eel Recruiting to the Upper St. Lawrence River and Lake Ontario

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## Abstract

We applied length frequency analysis (LFA) with multiple model inference to estimate the age structure of American Eel *Anguilla rostrata* recruiting to the upper St. Lawrence River and Lake Ontario system between 1975 and 2008. The LFA results were used to derive a composite relative abundance index for 48 cohorts from 1967 to 2004. The size of eel recruits was influenced by both year and season and consistently increased from July to October. Age composition and mean length at age varied greatly from year to year. On average, eels spent about 6 years in the lower St. Lawrence River before they recruited to Lake Ontario. A nonsymmetric distribution function, such as lognormal or Gamma function, was selected to describe length-at-age observations of American Eels. Recruiting cohorts appeared to be relatively strong from the late 1960s to the late 1970s but subsequently declined exponentially. Some recovery signs were found for the last 8 years, but cohorts have been weak since 1988. A validation study showed that the LFA with multiple model inference approach can successfully estimate the age structure from length frequency observations. Our results provide scientific support for underlying eel habitat restoration and protection efforts in Lake Ontario and the upper St Lawrence River.

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Age composition provides necessary information for understanding the biological processes of growth, mortality, recruitment, and migration of a fish population (Bagenal 1974; Weatherley and Gill 1987; Quinn and Deriso 1999). For in-

stance, knowing the age of a fish provides a clue to its longevity, maturity schedule, and growth patterns. Age determination can be obtained directly or indirectly. Direct age determination involves the evaluation of annual depositions in calcified

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structures (scale and otoliths), aided by validation experiments involving marked individuals or captive trials (Weatherley and Gill 1987). Although direct age determination is widely practiced, this approach is expensive and time-consuming and often requires lethal sampling. Some fundamental problems still constrain the ability to interpret ages from deposition patterns in solid tissues (Weatherley and Gill 1987).

Indirect age determination may provide a cost-effective alternative to direct aging, especially where assessments require estimation of age structure over a long time (Pauly and Morgan 1987). Length frequency analysis (LFA) evolved from the theory of mixture distributions and has been used as an indirect age determination to decompose a length frequency histogram into age groups (Hasselblad 1966; Macdonald and Pitcher 1979; Macdonald 1987). Length frequency analysis is based on the notion that a sequential series of modes in a length frequency observation may reflect the annual influx of new recruits over a distinct reproductive period (Weatherley and Gill 1987). It estimates the age composition of a fish population using information that can be collected at low cost through routine research surveys. In addition to many applications in fisheries research, LFA has recently been used to account for population growth and mortality (Özbilgin et al. 2004; Gökçe et al. 2007) and to back-calculate birth dates of some marine fish species (Andrade and Kinas 2004).

The American Eel *Anguilla rostrata* is a facultatively catadromous, semelparous species with a broad geographic distribution in the western North Atlantic Ocean and its connecting freshwater habitats (Helfman et al. 1984; Scott and Crossman 1998). The upper St. Lawrence River and Lake Ontario (USLR-LO) system provides a suitable freshwater habitat to accommodate somatic growth and gonadic development of American Eel populations and important ecological connections between the Laurentian Great Lakes freshwater and marine ecosystems. American Eel reproduction occurs only in the Sargasso Sea and the population habitats cover coastal marine, estuary, and freshwater systems in the eastern part of North America (COSEWIC 2006). Each year, juvenile eels (age-0 fish) hatched in the Sargasso Sea are transported by oceanic currents to the St. Lawrence River estuary (Bonhommeau et al. 2008; Dutil et al. 2009). Some juveniles swim upstream and recruit into the Lake Ontario eel population (Helfman et al. 1987; COSEWIC 2006). The journey from the spawning grounds to USLR-LO may take years and cover as much as 6,000 km. Whereas females migrate up the St. Lawrence River to Lake Ontario, males remain in the St. Lawrence estuary (Jessop et al. 2002; Cairns et al. 2004). Because the ascent up the St. Lawrence River is variable, eel recruitment to USLR-LO involves multiple age groups and likely responds to both biotic and abiotic environments over broad and diverse habitats (Knights 2003; MacGregor et al. 2008). Yellow juvenile eels may stay in USLR-LO up to age 25 years before they start to develop into maturing (silver) eels that descend the St. Lawrence River on their way to the Sargasso Sea for reproduction (COSEWIC 2006; MacGregor et al. 2008). Female silver eels from USLR-LO are the

largest and most fecund in the species' range, leading to the suggestions that these eels historically contributed a significant proportion of annual American Eel egg production at the Sargasso Sea spawning grounds (Casselman 2003; Tremblay 2004; COSEWIC 2006).

The annual average number of American Eels recruiting to USLR-LO was estimated to exceed 600,000 in the 1980s but then declined by more than 98% (DFO 2010). Although various triggers of this collapse have been proposed, the limited information on the age structure of recruiting eels has constrained robust analysis of the effects of environmental conditions on recruitment dynamics (Casselman et al. 1997; Haro et al. 2000; Jessop et al. 2002, 2004; Morrison and Secor 2003; Cairns et al. 2004; Machut et al. 2007; MacGregor et al. 2008). Recently, the species has been listed as endangered by the Province of Ontario, Canada. A better understanding of population dynamics of American Eel is needed for the development of a recovery plan for the species. Specifically, how do environmental conditions shape the age and size structures of the recruits? In this study, we used long-term observations of lengths of eels recruiting to the USLR-LO system to (1) examine seasonal and interannual variation in the size of recruiting eels, (2) estimate annual age composition using LFA, and (3) assess the cohort strength and temporal changes in population age structure.

## METHODS

*Data collections and statistical analysis.*—The upper St. Lawrence River is the river stretch upstream from the Moses-Saunders Power Dam (MSPD) to the estuary of Lake Ontario (Figure 1). Data used for this study were obtained from an Ontario Ministry of Natural Resources (OMNR) monitoring program on juvenile eels entering USLR-LO from the lower St. Lawrence River from 1975 to 2008. Between 1975 and 1986 juvenile eels were sampled using a net hung at the exit chute of an eel ladder on the MSPD. Beginning in 1987, an electronic counter monitored upstream eel migration over a ladder operated annually from mid-June to late October (Marcogliese and Casselman 2009). Mean daily counts of ascending eels during the 31-d migration peak between mid-July and mid-August have been used as a recruitment index for USLR-LO (Casselman et al. 1997; Marcogliese and Casselman 2009). In addition to the counts, biological measurements, including total length (to the nearest millimeter) and total weight (to the nearest gram), were made on subsamples of recruiting fish. Otoliths were collected during the monitoring periods but not aged completely yet. The 2006–2008 length-at-age data were retrieved from the OMNR eel monitoring dataset and used for a model validation of the LFA approach described below.

We first investigated how the size of the recruiting eels changed with season (i.e., month) and year using a two-way analysis of variance (ANOVA; SAS 2004). A post hoc Bonferroni multiple comparison was used (MULTTEST; SAS 2004) to examine seasonal variation in the marginal means of lengths of recruiting eels where appropriate.

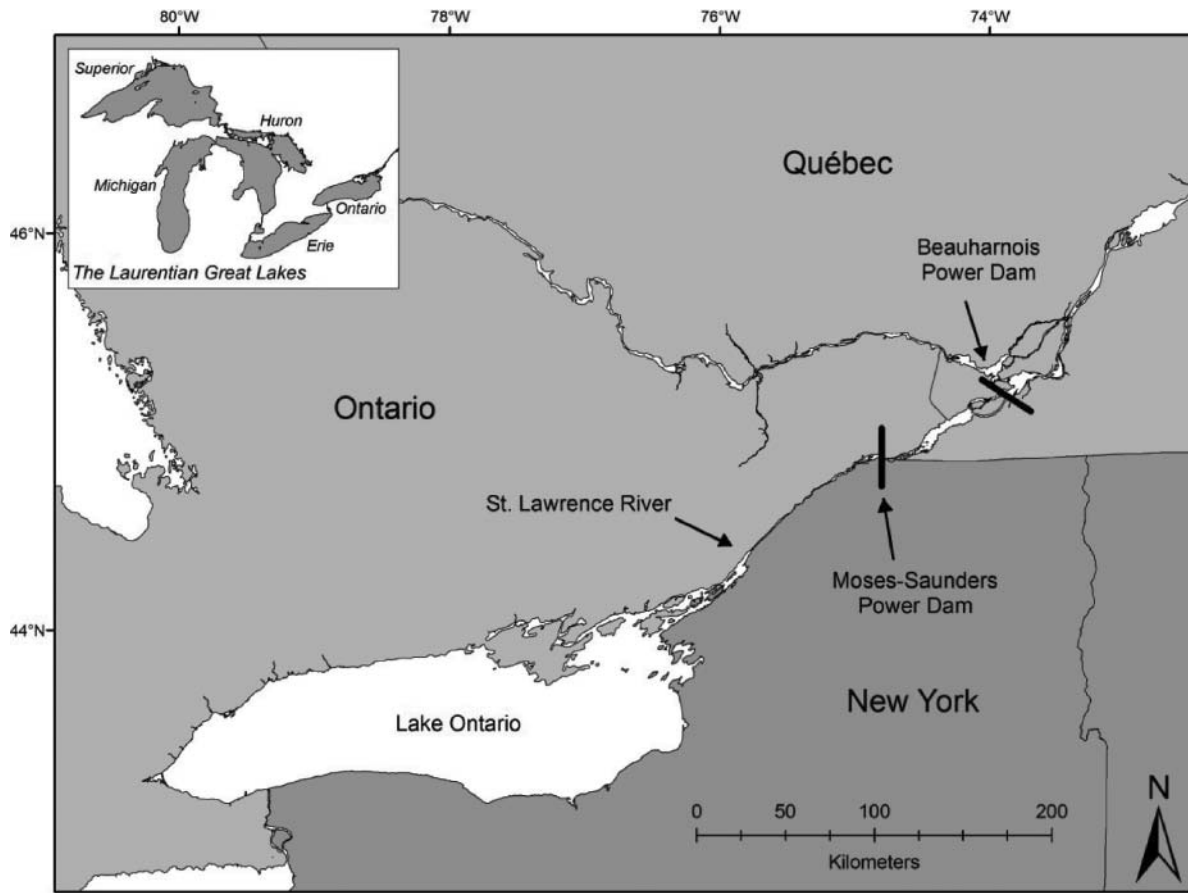


FIGURE 1. Map of the study area—the upper St. Lawrence River and Lake Ontario. Bars label two hydroelectric dams, including the Moses-Saunders Power Dam.

*Length frequency analysis modeling and validation.*—In LFA, a length frequency observation was assumed to consist of a fixed number ( $k$ ) of age groups. For each age-group  $i = 1, 2, \dots, k$ , a random variable of length ( $x$ ) has a definable probability density function of  $f_i(x)$ . Therefore, the observed length frequency is a mixture distribution  $g(x | \Theta)$  of  $k$  components of  $f_i(x)$  with mixing weights  $\pi_i$  that can be expressed as

$$g(x | \Theta) = \pi_1 f_1(x | \theta_1) + \dots + \pi_k f_k(x | \theta_k), \quad (1)$$

where  $\pi_1, \dots, \pi_k$  are mixing weights or proportions ( $0 \leq \pi_i \leq 1$  and  $\sum_{i=1}^k \pi_i = 1$ ;  $i = 1, \dots, k$ ), and  $\Theta$  and  $\theta$  are parameter vectors for the mixture and component distributions, respectively.

Length frequency analysis estimates these parameters through a maximum likelihood approach. Most fish length frequencies are observed with no age information, i.e. incomplete data (Du 2002), which results in a complicated likelihood function with a marginal distribution of fish length ( $x$ ) as follows:

$$L(\Theta) = \prod_{j=1}^n g(x_j | \Theta) = \prod_{j=1}^n \left[ \sum_{i=1}^k \pi_i f(x_j | \theta_i) \right], \quad (2)$$

where  $n$  is the number of observed individuals. To reduce difficulties in obtaining the maximum likelihood of equation (2), individual length observations can be grouped into several length intervals (e.g.,  $m$  groups with  $n_j$  counts in each group). The grouped length data ( $n_1, n_2, \dots, n_m$ ) have a multinomial distribution describing  $n_j$  draws from  $m$  categories with the probabilities of  $P_j(\Theta)$  ( $j = 1, 2, \dots, m$ ). Thus, the likelihood function, equation (2), for the group data, can be rewritten as

$$L(\Theta) = \frac{n!}{n_1! \dots n_m!} \{P_1(\Theta)\}^{n_1} \dots \{P_m(\Theta)\}^{n_m}, \quad (3)$$

where  $n = \sum_{j=1}^m n_j$ ,

and

$$P_j(\Theta) = \int_{a_{j-1}}^{a_j} g(x | \Theta) dx, \quad (4)$$

where  $a_{j-1}$  and  $a_j$  are upper and low boundaries for the length category  $j = 1, 2, \dots, m$ , and  $g(x | \Theta)$  is obtained from the equation (1). The maximum likelihood of equation (3) can be

evaluated by setting constraints on the parameter  $\theta_s$  and  $\pi_s$  in equation (1).

Macdonald (1987, 2008) provided elegant reviews on the LFA approach and developed a statistical analysis package, called MIX (<http://www.math.mcmaster.ca/peter/mix/mixdist.pdf>). A revised version of MIX for the R environment (<http://www.r-project.org/>) called RMIX was later released (Du 2002). The RMIX incorporates a two-step numerical method, expectation-maximization (Dempster et al. 1977) and Newton-Raphson, to compute the maximum likelihood estimation. It also was designed to fit a set of component distribution functions, such as binomial, Poisson and negative binomial, and to provide more flexible options on constraints of distribution parameters.

In this study, we used RMIX to decompose observed length frequency information into age compositions of juvenile American Eels recruiting to USLR-LO. We used the observed age range (age 3 to age 9 plus) to constrain the possible number of age-groups. After preliminary tests of different component distribution functions, we selected the interpretation of the mixture components by three continuous probability distributions: normal (N), lognormal (LN) and gamma (G). Following Du (2002), three constraints selected for the means of each distribution were means fixed at the observed values (MFX), means conforming to a growth curve (MGC), and means not specified (NONE). For MFX, we fixed mean lengths at ages 3–8 as the observed values; length at age 9 plus was treated as a parameter estimated in the model. For the MGC, we estimated length at age for age 3, 4, and 5 of fish using observed length-at-age data. Lengths at age 6–8 were derived from a von Bertalanffy growth equation constrained by the lengths of the first three age compositions (Du 2002). Length at age for fish aged 9 plus was estimated by the model. In addition, three constraints were applied to age-specific standard deviations: fixed (SFX), constant coefficient of variation (CCV), and no constraints (NONE). We used observed standard deviations of each age-group for the SFX scenario. Overall, 27 candidate models were constructed to combine with three component distribution functions, three mean constraints, and three standard deviation constraints. For all the models tested, the proportional parameters ( $\pi_s$  in equation (1) or age compositions) were freely estimated without any constraint.

We used Quasi-likelihood adjusted Akaike information criterion corrected by sample size (QAIC<sub>c</sub>) to select the best model among 27 models, following Burnham and Anderson (2002):

$$\text{QAIC}_c = -[2\log(L(\Theta)/\hat{\epsilon})] + \frac{2K(K+1)}{N-K-1}$$

$$\hat{\epsilon} = \frac{\chi^2}{df}, \quad (5)$$

where  $K$  is number of parameters,  $N$  is sample size,  $\chi^2$  is chi-square for model goodness of fit, and  $df$  is the degree of freedom for the  $\chi^2$ -statistic.

The QAIC<sub>c</sub> differences ( $\Delta_i$ ) between the model  $i$  (QAIC<sub>c*i*</sub>) and the best model with the minimum QAIC<sub>c</sub> (QAIC<sub>c<sub>min</sub></sub>) enabled model comparisons:

$$\Delta_i = \text{QAIC}_{c_i} - \text{QAIC}_{c_{\min}}. \quad (6)$$

Burnham and Anderson (2002) suggested a multiple model inference (MMI) strategy to make statistical inferences based on all or a subset of candidate models, i.e., multimodel averaging, rather than a single-best model. They also indicated that the multimodel averaging resulted in stabilized inference with less bias. To apply the MMI strategy for estimating the age composition parameter  $\pi_i$ , we first calculated the QAIC<sub>c</sub> weight ( $w_i$ ) for each model  $i$ :

$$w_i = \frac{\exp(-0.5 \times \Delta_i)}{\sum_i \exp(-0.5 \times \Delta_i)}. \quad (7)$$

Second, we derived the model-averaged estimate ( $\bar{\pi}$ ) of the age composition parameter  $\pi_i$  using the weight factor ( $w_i$ ) and the following equation:

$$\bar{\pi}_i = \sum_i w_i \times \pi_i. \quad (8)$$

Instead of using all candidate models, we selected a subset of models with a total QAIC<sub>c</sub> weight ( $\sum w_i$ ) greater than or equal to 0.95, and readjusted weight values within the model subset for the calculation of model averages (Burnham and Anderson 2002). Model validation was conducted to compare observed age structures from subsamples of the 2006–2008 OMNR's American Eel recruitment monitoring program and the model averaging estimates using a  $G$ -test statistic (Sokal and Rohlf 1995). The validation study provided confidence levels on applying the LFA approach to length frequency observations from 1975 to 2008 to derive time series of age composition of American Eel recruiting to Lake Ontario.

*Annual recruit-at-age and composite indices of cohort strength.*—We used the number of eels per day ascending the eel ladder during the 31-d peak period (see section 2.1 for details) and estimated age composition ( $\bar{\pi}$ ) to derive the daily average number-at-age of recruits to represent annual recruit-at-age from 1975 to 2008. We also calculated a composite index of cohort strength by averaging the number of recruits from age 3 to age 8 for each cohort observed in the study.

## RESULTS

### Temporal Patterns of the Sizes of American Eels Recruiting to Lake Ontario

A total of 9,769 young American Eels was recorded by their total length at the MSPD during 1975–2008 except for 4 years (1979, 1992, 1995, and 1996) when no samples were taken. The

TABLE 1. Bonferroni multiple comparisons of mean length (mm) of American Eel recruiting to Lake Ontario by month from 1975 to 2008. The values are the differences of monthly mean lengths in columns and those in rows, and an asterisk indicates statistically significant difference between two means, i.e., a negative number implying the column value is smaller than the row value.

	June	July	August	September
July	25.70*			
August	12.40	-13.30*		
September	-6.91	-32.60*	-19.30*	
October	-9.04	-34.70*	-21.40*	-2.13

annual sample size ranged from 35 (1989) to 1,209 (1981); body length ranged from 126 to 723 mm. A two-way ANOVA showed that total length of the recruits varied significantly by month ( $F_{4,107} = 25.17, P < 0.001$ ), year ( $F_{28,107} = 69.97, P < 0.001$ ),

and interaction of month and year ( $F_{75,107} = 7.35, P < 0.001$ ). Post hoc Bonferroni multiple comparisons showed that lengths increased with months from July to October (Table 1). However, the average length of recruiting eels in June was greater than that in July but not significantly different from that in August, September, and October.

**Length Frequency Analysis Modeling and Validation**

Of the 27 candidate models, the top six models ranked by QAIC<sub>c</sub> weight values were selected to produce multimodel averages with a sum of weight value of 0.96 for length frequency observations from 2006 to 2008 (i.e., the model validation period) (Table 2). Results of the G-statistic analysis indicated that the LFA with MMI approach for the selected models successfully predicted the observed age structure of American Eels ( $G_6 = 4.01, P > 0.50$ ) (Figure 2).

TABLE 2. Validation results of the LFA with MMI approach to estimating age compositions using observed length frequency of American Eels recruiting to Lake Ontario from 2006 to 2008. Codes include the following: Dist = probability distribution function, N = normal, LN = lognormal and G = gamma. Mean configurations (Mean) are freely estimated (NONE), von Bertalanffy growth curve (MGC), and fixed means (MFX). Variance constraints (SD) are no constraints (NONE), constant coefficient of variation (CCV), and fixed constraints (SFX). The values of  $\chi^2$  and QAIC were  $\chi$ -statistic and Quasi-likelihood adjusted Akaike information criterion; and  $\Delta_i$  and  $w_i$  were QAIC differences and weight between the *i*th model and the best model. Numbers in bold italics identify the model selected as one of a subset of models with sum of  $w_i \geq 0.95$ .

Model structure			2006–2008				
Dist	Mean	SD	df	$\chi^2$	QAIC	$\Delta_i$	$w_i$
N	NONE	NONE	25	31.26	55.80	20.30	0.000
LN	NONE	NONE	23	29.66	42.64	7.14	<b>0.018</b>
G	NONE	NONE	24	29.40	49.14	13.64	0.001
N	NONE	SFX	32	33.32	47.97	12.47	0.001
LN	NONE	SFX	29	33.21	45.08	9.59	0.005
G	NONE	SFX	30	33.05	46.42	10.92	0.003
N	NONE	CCV	29	31.41	44.52	9.03	0.007
LN	NONE	CCV	31	34.13	54.85	19.35	0.000
G	NONE	CCV	29	33.67	47.37	11.88	0.002
N	MFX	NONE	31	31.69	42.13	6.63	<b>0.023</b>
LN	MFX	NONE	29	29.35	41.55	6.05	<b>0.030</b>
G	MFX	NONE	29	31.59	44.77	9.27	0.006
N	MFX	SFX	38	33.79	49.79	14.29	0.000
LN	MFX	SFX	35	34.13	50.13	14.63	0.000
G	MFX	SFX	35	34.14	50.14	14.64	0.000
N	MFX	CCV	35	31.79	47.79	12.29	0.001
LN	MFX	CCV	35	33.85	47.85	12.35	0.001
G	MFX	CCv	35	33.55	45.55	10.05	0.004
N	MGC	NONE	30	34.61	46.66	11.17	0.002
LN	MGC	NONE	28	30.30	54.43	18.93	0.000
G	MGC	NONE	28	30.02	35.50	0.00	<b>0.622</b>
N	MGC	SFX	36	35.28	47.28	11.78	0.002
LN	MGC	SFX	32	36.41	48.54	13.04	0.001
G	MGC	SFX	34	34.19	46.32	10.82	0.003
N	MGC	CCV	36	34.34	42.34	6.84	<b>0.020</b>
LN	MGC	CCV	34	35.77	37.37	1.87	<b>0.244</b>
G	MGC	CCV	34	35.31	46.15	10.65	0.003

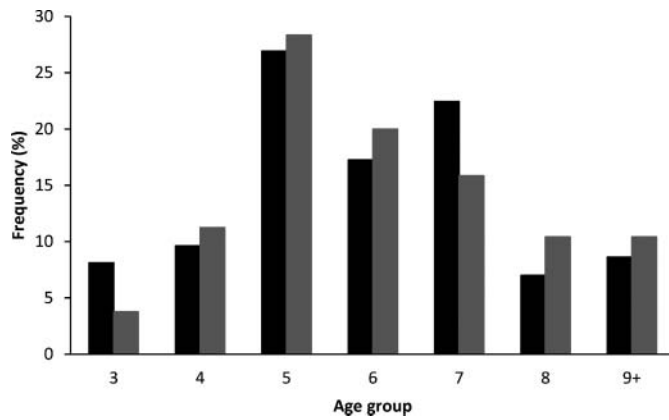


FIGURE 2. Comparison of the observed (black bar) and predicted (grey bar) age structure for American Eel recruiting to the upper St. Lawrence River during 2006–2008. A  $G$ -test showed that age-specific differences were not significant at  $\alpha = 0.05$ .

### Age Structure and Cohort Strength

The validated approach, i.e., the LFA with MMI, was applied to break down the length frequencies to age structures of

American Eel recruiting to USLR-LO from 1975 to 2008. In about 43% of 30 years, QAIC<sub>c</sub> weightings pointed to LN-NONE-SFX as the best models to derive age structure, followed by G-MFX-CCV (33%), G-MGC-CCV (30%), G-NONE-CCV (27%), G-MGC-NONE (27%) and N-MGC-CCV (27%) (Table 3). For the 30 years, about 70% of selected models were non-symmetric: either gamma (G) or lognormal (LN), and about 40% were configured with constant coefficient of variance (CCV), followed by about 35% of fixed variance (SFX) and 25% of no variance constraints (NONE). However, for the mean configuration, about 37% of the selected models were not constrained by means (NONE), about 34% were configured with the von Bertalanffy growth curve (MGC), and about 29% had fixed means at observed values (MFX).

Estimated mean age composition ( $\bar{\pi}$ ) rose from the mid-1970s to the mid-1990s, plateaued until 2003, and then declined (Figure 3). The overall average age  $\pm$  SE was  $6.80 \pm 0.16$  years, showing a 60% increase from the mean age  $5.05 \pm 0.19$  in 1978 through  $8.18 \pm 0.13$  years old in 1994 (lower panel of Figure 3). Prior to 1987, fish under 5 years of age represented 26% of the recruits ( $CV = 45\%$ ). In 1988–2005, this number fell to 4% ( $CV = 57\%$ ). Since 2006, it has increased to 22%

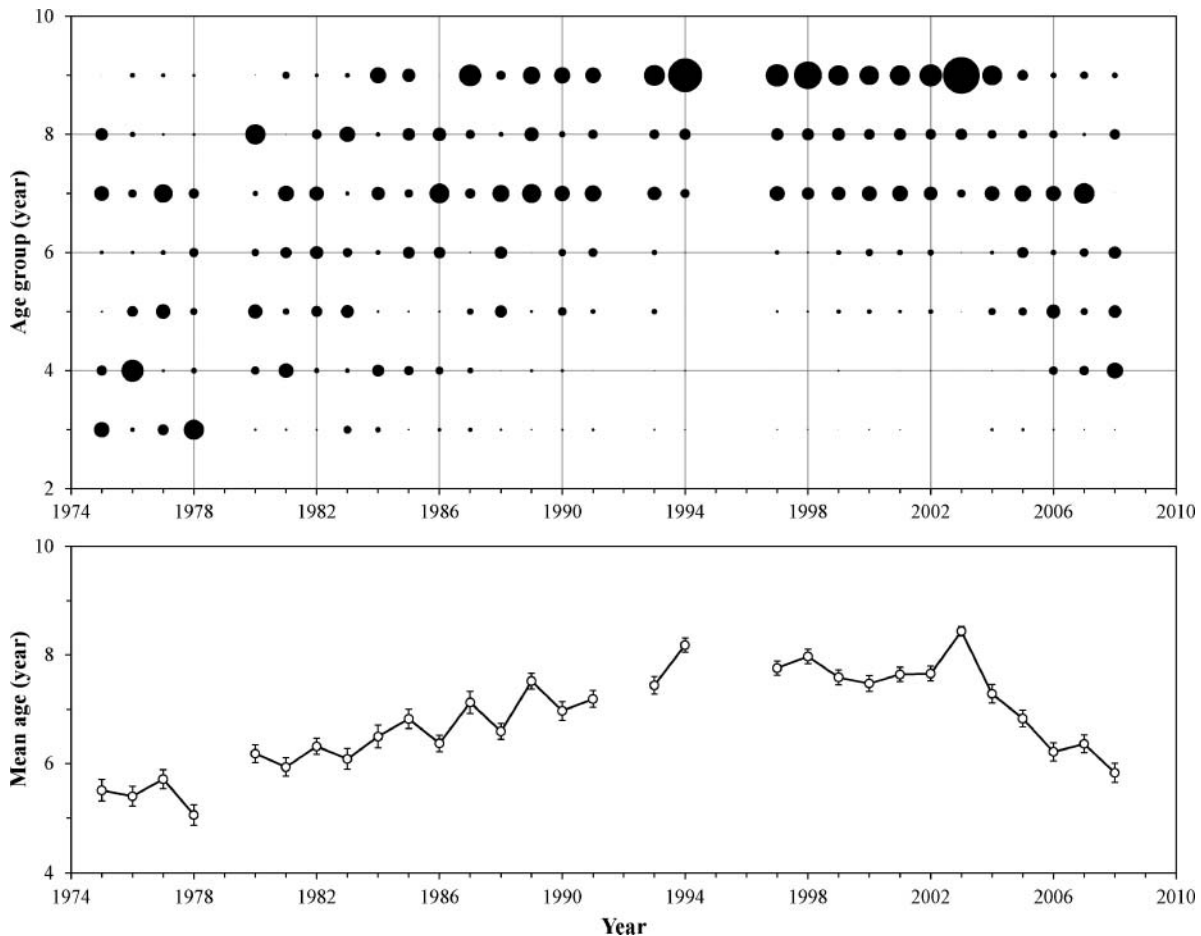


FIGURE 3. Length frequency analysis estimates of age composition (upper) and mean age ( $\pm$  SE; lower panel) of American Eel recruiting to Lake Ontario from 1975 to 2008. Age proportion for age-group 9+ was represented as age 9.

TABLE 3. Weights of QAIC<sub>c</sub> for the validated LFA with MMI approach to estimating age composition of American Eels recruiting to Lake Ontario from 1975 to 2008. See Table 2 for label definitions. Numbers in bold italics identify the model selected as one of subset models with sum of  $w_i \geq 0.95$ . See text for a description of MMI procedure.

Distribution	N	LN	G	N	LN	G	N	LN	G	N	LN	G	N	LN	G	N	LN	G	N	LN	G	N	LN	G	N	LN	G	
Mean	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE	NONE
SD	NONE	NONE	NONE	NONE	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	SFX	
1975	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1976	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1977	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1978	<b>0.51</b>	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1980	0.00	0.00	0.01	0.00	0.00	<b>0.05</b>	0.00	0.00	0.00	<b>0.05</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	<b>0.15</b>	
1981	<b>0.06</b>	<b>0.66</b>	<b>0.19</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1982	<b>0.10</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	<b>0.26</b>	0.01	<b>0.02</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1983	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1984	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	<b>0.07</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1985	0.00	<b>0.37</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	<b>0.02</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1986	<b>0.03</b>	<b>0.06</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1987	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1988	0.00	0.00	0.00	0.00	0.00	<b>0.44</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1989	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1990	0.01	<b>0.43</b>	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	<b>0.19</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1991	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1993	0.00	0.00	0.00	0.00	0.00	<b>0.03</b>	<b>0.06</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1994	0.00	0.00	0.00	0.00	0.00	<b>0.02</b>	<b>0.04</b>	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1997	0.00	0.00	0.00	0.00	0.00	<b>0.03</b>	<b>0.63</b>	0.00	0.00	<b>0.04</b>	0.00	<b>0.02</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1998	0.00	<b>0.01</b>	0.00	0.00	0.00	<b>0.08</b>	<b>0.41</b>	<b>0.08</b>	0.00	<b>0.05</b>	0.00	<b>0.02</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
1999	0.00	<b>0.81</b>	0.01	0.01	0.00	<b>0.03</b>	<b>0.02</b>	<b>0.02</b>	0.00	<b>0.05</b>	0.00	<b>0.05</b>	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
2000	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
2001	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
2002	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
2003	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
2004	0.00	0.00	0.00	0.00	0.00	0.00	<b>0.04</b>	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
2005	0.00	0.00	0.01	0.00	0.00	0.00	<b>0.51</b>	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
2006	<b>0.06</b>	0.01	<b>0.01</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
2007	0.00	0.00	0.00	0.00	0.00	0.00	<b>0.04</b>	<b>0.05</b>	<b>0.02</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
2008	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Number of year observed	5	6	3	6	3	6	7	8	6	3	3	5	4	7	5	7	10	4	5	8	7	4	5	8	7	9		
Importance (%)	16	20	10	20	43	23	20	23	26	10	10	16	13	23	16	23	33	13	16	26	23	13	16	26	23	30		

(CV = 31%). The proportion of fish older than 7 years exceeded 50% in 1993–2003 with an average of 63% (CV = 18%). Thus of three age clusters (young: <5, middle: 5–7, elder: >7), the percentages varied significantly ( $F_{2,89} = 31.42$ ,  $P < 0.001$ ).

An ANOVA showed that the daily average number of age-specific recruits in USLR-LO varied greatly among years (one-way ANOVA:  $F_{29,209} = 9.41$ ,  $P < 0.0001$ ; Figure 4). Over the 30-year period, age-7 fish exhibited the highest number of recruits (at least 35% higher than any other age groups), followed by age-8 fish (Figure 5). During the years of high recruitment (1982–1983), about 71% of the recruits were ages 5–8. The cohorts from the late 1960s through the late 1970s were relatively stronger than the rest of the time series, exhibiting exponential decline since the late 1970s. However, there seemed to be an improving trend for the cohorts of 1998–2004 compared with those of the early 1990s (Figure 6).

Multimodel-averaged length at age of the recruiting eels varied year by year. The mean lengths of fish age 3–5 appeared to decrease from 1975 to 1978 but increased for ages 6–8 (Figure 7). For all age groups, the mean length seemed to increase from the early 1980s to the middle 1990s and decrease from 1997 to 2008 except for age-9+ fish. There was a noticeable decrease for age-3 to age-8 fish in 2003 compared with the adjacent years. The lengths of fish age 3–5 in 1989 were similar.

## DISCUSSION

A significant seasonal pattern of length distribution of recruiting eels in the USLR-LO system was observed in this study. Fish length increased with month from July through October, but eels were largest in June and comparable to those in October. Large individuals in the early migration season were also recorded among glass eels (the transparent, postlarval stage) in Little Egg Inlet, New Jersey (Sullivan et al. 2006) and the lower Roanoke River, North Carolina (Overton and Rulifson 2009). At least two possible mechanisms might explain the observed migration behavior of American Eel: temperature dependence and growth driven. Under the temperature-dependent mechanism, young and small eels may ascend the MSPD at warm temperatures (i.e., July and August) whereas old and large eels ascend at cool temperatures (June, September, and October). The growth-driven mechanism could account for the first peak of fish length in June, representing “leftover”, large fish from the previous years’ recruitment. Additionally, subsequent recruits that progressively increased in length could result from the addition of newly arriving small individuals that grow throughout the summer and fall. To test these mechanisms, tag-recapture experiments and ecological investigations of American Eel recruit abundance and environmental variables along the St. Lawrence River are needed.

Many studies have used the Akaike information criterion or its variants to select the best model for parameter estimates. However, model selection focusing on a single best model could

result in variation among years, increasing model selection uncertainty. The MMI approach is an uncertainty-reduced and less-biased estimating procedure in which the main characteristics of length-at-age distribution and growth patterns of the recruiting eels can be clearly identified.

In this study, we observed that length-at-age distribution of American Eel strongly favors a nonsymmetric shape, such as lognormal or Gamma curves (Limpert et al. 2001), suggesting that a few individuals at each age-group can grow much faster and reach much larger sizes than the other eels. Such relative fast growth for a small number of individual eels can skew the length-at-age distribution to the right (a long right tail), resulting most likely in the large variance of length at age commonly observed for the species. The rejection of the models with fixed mean configuration for most study years suggests that the mean length at each age varies year by year but follows the von Bertalanffy growth function for some years. However, the variance of the distribution can be either fixed or modeled by a function of the mean.

The ages of recruits reveal the time that American Eels stay in the St. Lawrence River and Lake Ontario. American Eels are typically age 1 in their year of arrival in continental waters (Jessop et al. 2002; Powles and Warlen 2002; Morrison and Secor 2003; Cairns et al. 2004). Eels that recruit to Lake Ontario were estimated to be 7 years old, suggesting that the species, on average, spends about 6 years in the waters downstream of the MSPD and about 8–18 years in the USLR-LO. This scenario assumes that silvering eels leave the region at 15–25 years of age (MacGregor et al. 2008; de Lafontaine et al. 2009). Because American Eels spend about two-thirds of their life time in the USLR-LO, this region is an important freshwater habitat for the species. The condition of Lake Ontario determines the quality and quantity of matured (silver) eels and population sustainability of the species (COSEWIC 2006).

Understanding fish cohorts is important to model population dynamics and to assess how fish spawners and environmental factors influence recruitment dynamics. Unfortunately, no previous study has been conducted to estimate the year-class strength for American Eel in the St. Lawrence River and Lake Ontario likely due to the complex life history, long-distance migratory behavior, and broad spatial distribution of the species (Helfman et al. 1987; Casselman 2003; Knights 2003; Bonhommeau et al. 2008). Based on limited information, we estimated a composite index of cohort strength and generated general patterns of eel recruitment dynamics, including abundances and growth of age-1 glass eels entering the system from the Sargasso Sea to the St. Lawrence River before the eels recruit to Lake Ontario. Collecting information on environmental conditions and population dynamics of other species in the St. Lawrence River during the modeled period will help to understand the impacts of biotic and abiotic factors on migration behavior and early survivorship of eels. In addition, the estimated index also provides important information to study age structures and population dynamics of American Eels in Lake Ontario. The derived cohort strength



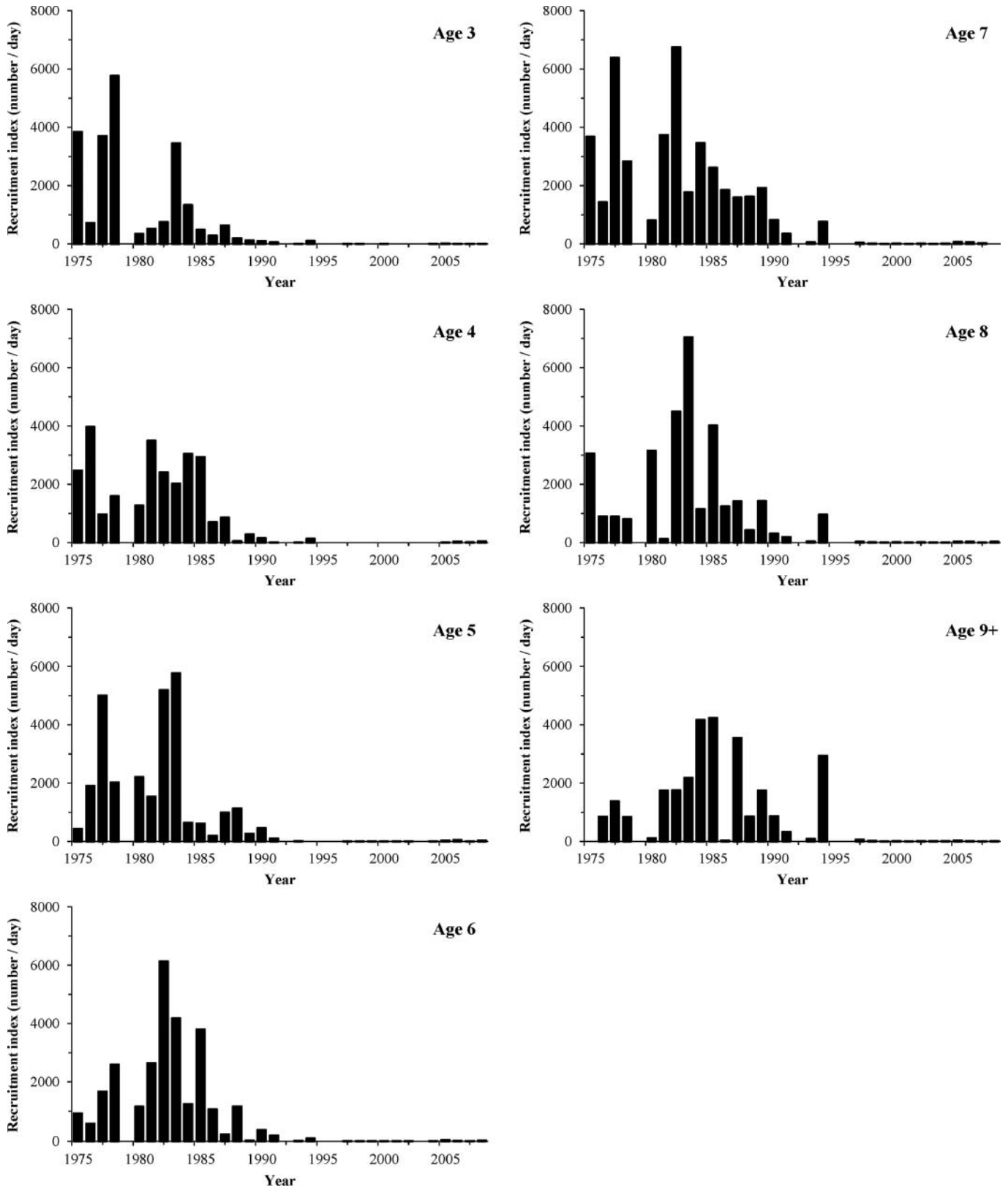


FIGURE 4. Mean age-specific number of eels per day recruiting to Lake Ontario from 1975 to 2008 during the 31-d peak period of recruitment.

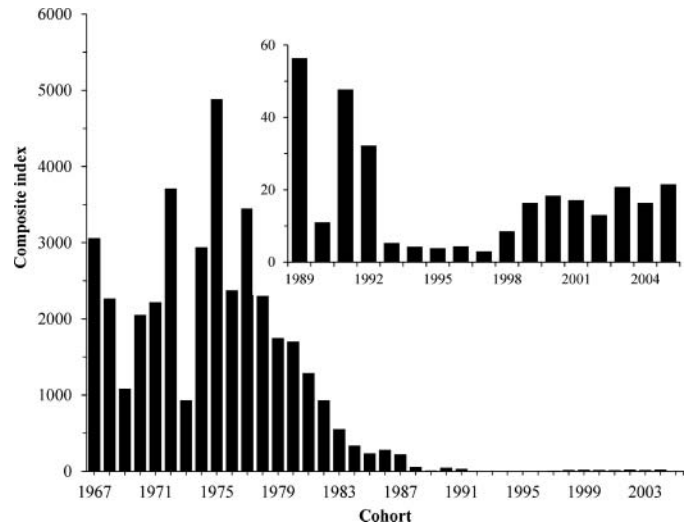
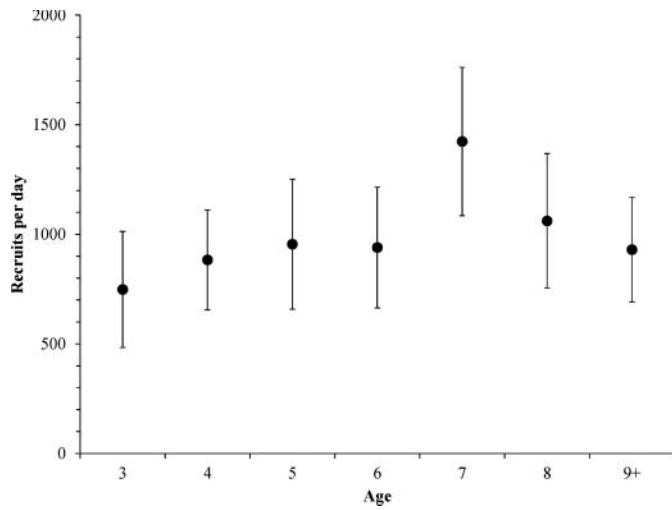


FIGURE 5. Estimated average recruits with standard error (bars) per day of American Eel in USLR-LO system over 1975–2008. The age-specific daily recruits were calculated by the estimated age composition and recruitment index at a 31-d peak period between mid-July and mid-August.

FIGURE 6. The estimated cohort strength (composite index) of American Eel recruiting in USLR-LO system over time.

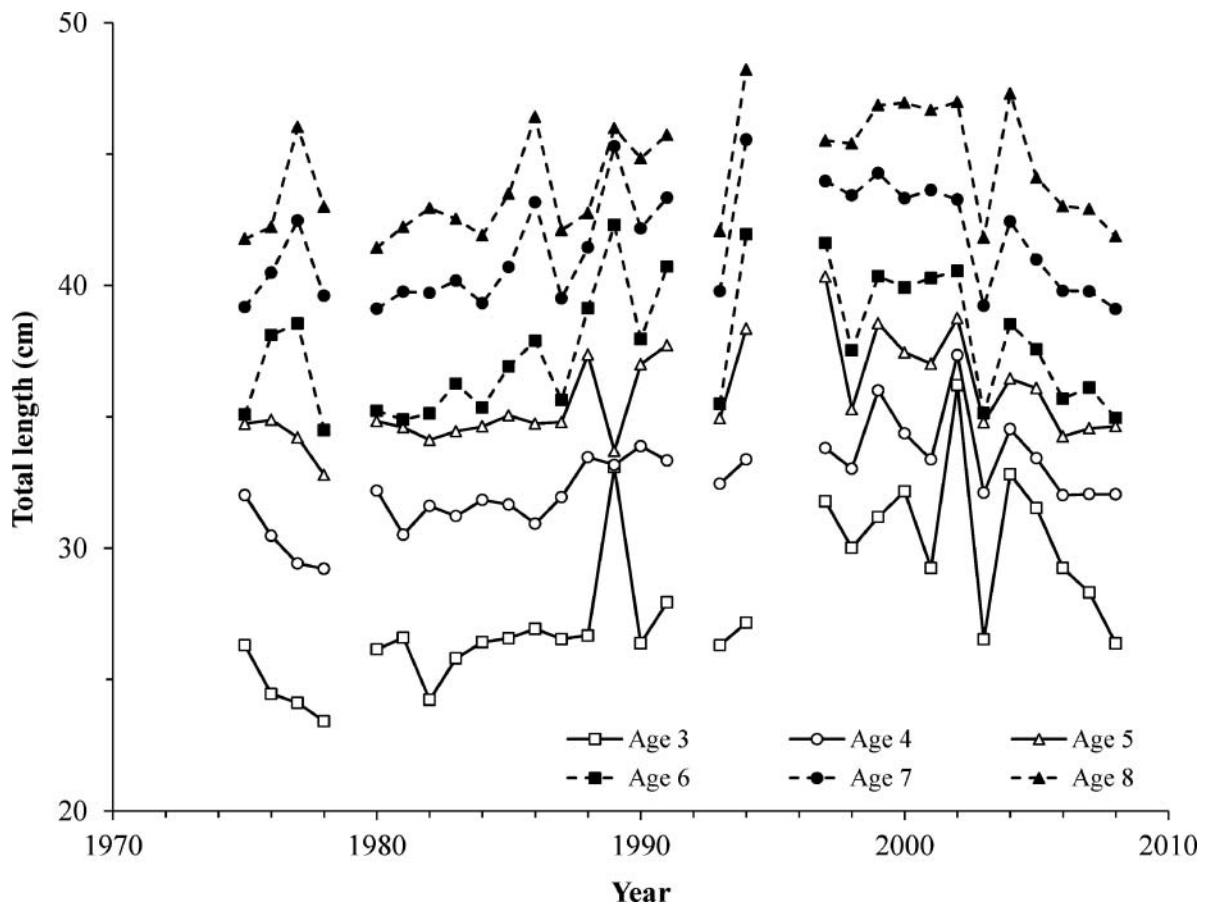


FIGURE 7. Time series of estimated length at age (3–8) of American Eel recruiting in USLR-LO system from 1975 to 2008.

can potentially aid in estimating the historical age-specific abundance, natural and fishing mortality rate, and other ecological parameters that are essential for understanding the eel population and establishing recovery plans for the USLR-LO region.

Regardless of some limitations of the LFA analysis (e.g., sensitivity to small sample size and assumption about age-group and probability density functions), this study successfully estimated fish age structures from length frequency observations. Andrade and Kinas (2004) found that underestimating age proportion was likely associated with the age groups with small sample sizes. Nevertheless, the LFA has proven to be much lower cost and less labor than processing and reading annulus marks on fish calcified structures, such as scales or otoliths. For future LFA applicability, we recommended that comparison of age composition between model-derived information and otolith reading throughout the entire sampling period would be desirable to compliment both methodologies of monitoring and assessing fish population dynamics impacted by increasing anthropogenic activities.

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