

Spawning dynamics of American shad (*Alosa sapidissima*) in the St. Lawrence River, Canada–USA

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Abstract – The most northerly population of American shad (*Alosa sapidissima*), located in the St. Lawrence River, is considered vulnerable because of low population abundance and limited spawning habitat located at the upstream extent of the population's anadromous migration. Here, we aimed to establish the temporal and spatial extent of spawning based on a novel hatch-date analysis of juveniles. Spawning activity lasted from early May to early July. We found that juveniles captured downstream during the summer hatched later in the year than those captured further upstream. As a result, younger juveniles were distributed somewhat further downstream. In addition, we found significant multimodality in hatch-date distributions at midstream and downstream sampling stations. Together, these results provide evidence that the 2-month spawning period involved numerous spawning events that progressed in a downstream direction as the season advanced, rather than being restricted to upstream sites over the spawning season.

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Key words: alosine clupeid; hatch-date analysis; multiple spawning events

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Introduction

The anadromous American shad (*Alosa sapidissima*) ranges from the St. Lawrence River, Canada, to the St. Johns River, Florida (Limburg et al. 2003). From their overwintering grounds on the Scotian shelf (Dadswell et al. 1987), the St. Lawrence population undertakes an annual spring migration of approximately 2000 km to reach its spawning grounds in the vicinity of Montreal, Québec (Fig. 1). This population has suffered severe reductions, already recognised as early as the late 19th century (Montpetit 1897) and continuing through the 20th century, with no sign of recovery (Provost et al. 1984). The reasons for this decline are probably numerous, but exploitation during the spring migration and the construction of multiple hydroelectric dams in the vicinity of Montreal and in the Ottawa River probably played a major role (Provost et al. 1984). There are presently two known spawning areas in the St. Lawrence River and its tributaries, both located approximately 260 km upstream from the St.

Lawrence estuary and found immediately downstream of dams. One is located in the Ottawa River at Carillon (Point Fortune) on the southwest shore at the Ontario–Quebec border downstream of a dam built in 1882 (Provost et al. 1984). A second spawning area is located in the vicinity of Montreal in the Rivière-des-Prairies below a dam built in 1928 (Bilodeau & Masse 2005). Prior to dam construction, American shad were potentially capable of migrating as far upstream as Ottawa on the Ottawa River, 125 km beyond the Carillon dam (Provost et al. 1984). The historical extent of upstream migration in the St. Lawrence River, beyond Montreal and up to the outlet of Lake Ontario, a total distance of 290 km, is unknown. Given the low abundance of the population through much of the 20th century, the loss of potentially significant spawning grounds upstream of contemporary dams and the fact that only two spawning areas are presently known, American shad is one of 11 species listed as vulnerable under Québec legislation on threatened and endangered species (MRNF, 2009).

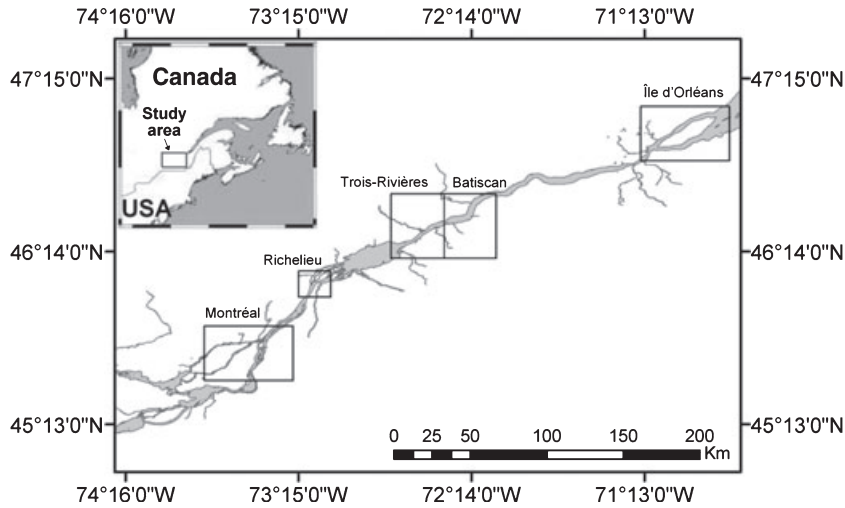


Fig. 1. Location map of the St. Lawrence River, illustrating the major sectors included in the sampling of juvenile American shad.

American shad are repeat spawners in the northern part ($>32^{\circ}\text{N}$) of their distribution along the east coast of North America (Leggett & Carscadden 1978). Under high levels of variance in mortality of the youngest life-history stages, such iteroparity forms part of the bet-hedging reproductive strategy that trades off a higher mean fitness in favour of a lower variance in fitness under environmental uncertainty (Philippi & Seger 1989). Another manifestation of bet-hedging is batch or serial spawning, whereby females spawn on several occasions and at different sites during the same reproductive season. In American shad, batch spawning has been observed in both semelparous (Edisto River) and iteroparous (York and Connecticut Rivers) populations (Olney et al. 2001). Evidence for batch spawning is based on the simultaneous observation of developing and postovulatory follicles in females captured at different points in their migration. These authors proposed that batch spawning increases the probability of finding favourable conditions for the survival of the most vulnerable life-history stages by dispersing them over greater spatial and temporal scales (Olney et al. 2001). Alternatively, different groups of fish, associated with different spawning events in space or in time, may also exist within the same river system (Hendry & Day 2005).

Our objective in this study is to establish the temporal and spatial extent of spawning by American shad in the St. Lawrence River. Although only two spawning areas have been identified, there are numerous sites throughout the St. Lawrence River where spawning by American shad is suspected to occur based on the physical and biological characteristics of the sites. Bouchard (1976) identified 16 potential spawning sites for American shad over the lower 120 km of the river. Putative spawning sites may also

exist in the Sainte-Anne, Batiscan and Richelieu rivers, as well as in the St. Lawrence fluvial lakes (Fig 1) (Provost et al. 1984). Provost (1987) proposed the existence of distinct populations among the tributaries of the St. Lawrence River based on the phenotypic characteristics of migrating adult fish.

To achieve this objective, we captured young-of-the-year shad throughout the St. Lawrence River to obtain otoliths for aging and hatch-date analysis. We tested the null hypothesis that all shad spawn uniquely in the vicinity of Montreal. Given this scenario and conservatively assuming downstream movement of larvae and juveniles (Limburg 1996), we predicted our first captures to include the youngest larvae hatched in the vicinity of Montreal, with age increasing over time in a downstream direction in concert with the downstream displacement, either active or passive, of juveniles. As such, we expected juveniles collected downstream to have hatched earlier in the season than juveniles captured further upstream. The alternative observation, whereby juveniles collected downstream hatched later in the season than juveniles collected upstream, would indicate the presence of multiple spawning events occurring downstream of known spawning sites in the vicinity of Montreal. The existence of multiple spawning events would also be expected to generate bi- or multimodal hatch-date distributions of juvenile shad at specific sampling stations.

Materials and methods

Study area and sampling

We sampled three to six sites (22 total) in each of five areas between Montreal and Ile d'Orleans, a distance

of about 260 km (Figs 1 and 2). Each site was sampled at several stations (Fig. 2). Sampling sites were clustered in three major regions for some subsequent analyses (the upstream region encompassing the Montreal and Richelieu sampling sites, the downstream region in the vicinity of Île d'Orléans and the midstream region encompassing the Trois-Rivières and Batiscan sampling sites). Samples were obtained during seven sampling occasions that took place from 14 June to 6 September 2006. One field team sampled upstream sites and a second team sampled midstream and downstream sites. Teams worked simultaneously and the weekly sampling occasions lasted on average 3 days.

Larval and juvenile collections

Larval American shad were collected with a 75-cm diameter pelagic trawl (500- μ m mesh) and juveniles (postmetamorphic) were caught with a 10-m beach seine (2-mm mesh). Trawling took place between 14 June and 5 July and seine fishing was conducted during the entire sampling period. Trawling consisted of a 10-min tow in the upper 2 m of the water column. All specimens were preserved in 95% ethanol for subsequent analyses.

Laboratory methods

Species identification and otolith extraction

We distinguished American shad from other clupeids (mostly alewife *Alosa pseudoharengus*) with identification keys (Jones et al. 1978 and Provost et al. 1984) and genetic analysis in the case of very small individuals. We used a restriction fragment length polymorphism technique to discriminate between shad and alewife. We extracted DNA with the salt technique described by Aljanabi & Martinez (1997) and amplified a segment of 609 base pairs of the mitochondrial *cytb* gene. The primers used for the PCR amplification were (L1-600) 5'-GGG TTG TTT GAT CCT GTT TCG TG-3' and (H2-600) 5'-AAA ACC ACC GTT GTT ATT CAA CTA CA-3'. The amplified segment was digested with the *Hae*III (5'-GG ↓ CC-3') restriction enzyme and afterward the fragments were counted on 2% agarose gels to discriminate between American shad and alewife. The American shad has two restriction sites in this segment that produce three fragments and the alewife has one restriction site that produces two fragments (F. Martin, F. Colombani and J.J. Dodson, unpublished data).

Altogether, we captured 3526 clupeids including 187 alewives and one gizzard shad (*Dorosoma*

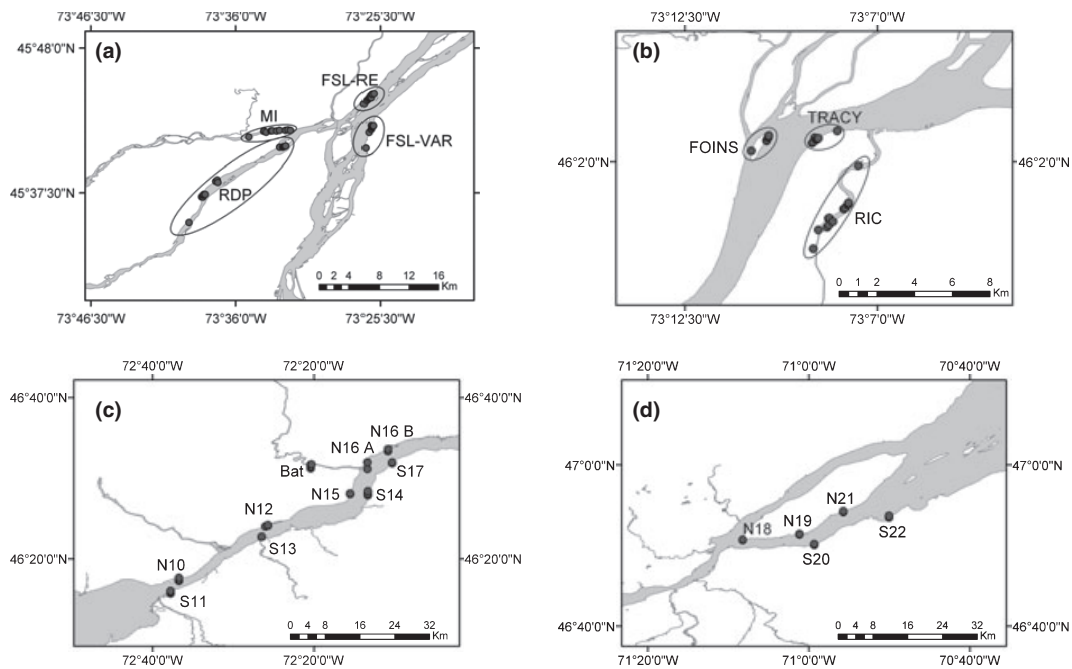


Fig. 2. Detailed illustration of sampling sites within the St. Lawrence River. (a) Sampling sites in the vicinity of Montreal: RDP – Rivière-des-Prairies, MI – Rivière-des-Mille-Îles, FSL-VAR – St. Lawrence R. near Varennes, FSL-RE – St. Lawrence R. near Repentigny. (b) Sampling sites in the vicinity of the Richelieu River: TRACY – south shore of the St. Lawrence R., FOINS – north shore of the St. Lawrence R., RIC – Richelieu R. (c) Sampling sites in the vicinity of Trois-Rivières and Batiscan: N – St. Lawrence R. north shore sampling sites, S – St. Lawrence R. south shore sampling sites, BAT – Batiscan R. (d) Sampling sites in the vicinity of Île d'Orléans: N – St. Lawrence R. north shore, Île d'Orléans, S – St. Lawrence R. south shore.

cepedianum). Total lengths of a subsample of 2259 shad were measured to the nearest 0.1 mm and sagittal otoliths of a subsample of 322 fish were extracted and mounted on microscope slides with Crystal Bond glue. We focused the study on five sampling events occurring between 14 June and 27 July. Length frequency distributions indicated that juveniles >90 mm total length, a size attained by mid-August, were apparently capable of avoiding the fishing gear, potentially biasing the reconstruction of hatch dates. A maximum of 50 juveniles per sampling event were measured and 5–15 fish were randomly selected for otolith extraction. Otoliths were polished with a series of increasingly fine lapping papers and daily growth increments (Savoy & Crecco 1987) were counted using a microscope with video attachment at 1000× under oil immersion. For larval otoliths, which are nearly circular, counts were made along the maximum radius and counts on juvenile otoliths were made along the major posterior axis. Every otolith was analysed two or three times by the same reader (E. Maltais) with fish identity hidden for every reading. Otoliths of 89 shad were rejected due to breakage, lack of clarity or when two independent readings differed by more than 15% of the mean age.

Statistical analyses

Hatch-date analysis

We used date of capture to calculate date of hatching for each of 233 larvae and juveniles for which age estimates were available. To extend the hatch-date analysis to the total sample of fish, we then estimated age (and hence hatch dates) of fish for which no otoliths were examined based uniquely on their size and date of capture. We first clustered the sample of 233 fish into four groups based on the length of fish, date of capture and their interaction. Four clusters were identified by the cubic clustering criterion of Sarle (1983) and by the pseudo *F*-statistic of Calinski & Harabasz (1974). The dates separating hatch dates into four clusters were determined by minimising the error of reclassification obtained with the leave-one-out cross-validation technique derived from a quadratic discriminant function (Huberty 1994). A total of 1520 combinations of four hatch-date clusters were tested. The choice of a quadratic function was motivated by the fact that the covariance matrices were heterogeneous between clusters. The four clusters that minimised reclassification errors (73.8% of observations were successfully reclassified) encompassed the following hatch dates: 22–28 May ($n = 9$, reclassification success = 66.7%), 29 May–5 June ($n = 78$, reclassification success = 76.9%), 6–19 June ($n = 132$, reclassification success = 72%), 20–29 June ($n = 14$, reclassification success = 78.6%).

The relationship between age and total length (TL) of fish whose age was estimated from otoliths and clustered in hatch-date cluster j was best described by the Gompertz growth model:

$$TL_{ij} = a * \exp \left\{ - \exp \left[\left(- \sum_{j=1}^4 k_j C_j \right) * \left(\text{age} - \sum_{j=1}^4 b_j C_j \right) \right] \right\} + \varepsilon_{ij}.$$

The variable C_j is an indicator variable taking the value 1 if fish belongs to cluster j and 0 if not, $j = 1, \dots, 4$. This growth model was adjusted simultaneously over all data of the four clusters. Within cluster j , this model reduced to the following form:

$$TL_{ij} = a * \exp \left\{ - \exp \left[-k_j (\text{age} - b_j) \right] \right\} + \varepsilon_{ij},$$

where parameter a is the asymptotic total length (a was kept constant for all fish), parameter b corresponds to age at the inflexion point, and parameter k is the growth rate to reach asymptotic length.

Using the inverse regression method, we estimated the age associated with a specific total length of all fish that were measured but for which otoliths were not read:

$$\widehat{\text{age}}_{ij} = \hat{b}_j - \frac{\log[\log(\hat{a}_j/TL_{ij})]}{\hat{k}_j}.$$

For fish i , we thus had an estimate of its age if this fish belong to cluster j , $i = 1, \dots, 4$ (age_{ij}). Moreover, from the quadratic discriminant function described previously, we had an estimate of the probability that this fish belonged to each cluster (\hat{p}_j). By Bayes' theorem, the age of fish i is thus estimated as a weighted average of the four predictions, i.e.,

$$\widehat{\text{age}}_i = \sum_{j=1}^4 \hat{p}_j \widehat{\text{age}}_{ij}.$$

The standard error of this estimate was calculated using the delta method (Oehlert 1992).

Once the estimation of age was done, we subtracted age from date of capture to estimate hatching date. Two weighted regression models were used to explain (i) the distribution of hatch date as a function of site and date of capture and (ii) the age of fish as a function of the same variables. In these regression models, each observation was weighted by the inverse of the variance of the age prediction, calculated by the delta method. All of the foregoing statistical analyses were conducted with SAS (SAS Version 9.2; SAS Institute, Cary, NC, USA).

The frequency distribution of hatching dates calculated from fish captured over several months required correction as the mortality suffered by a cohort

increases in concert with the time spent in the system. As such, the frequency of hatching dates of older fish at capture tend to be underrepresented in the population relative to birth dates of younger fish at capture. The frequency distribution was corrected using the mean mortality rates observed by Crecco et al. (1983) in the Connecticut River between 1979 and 1884: 0.218 day⁻¹ for fish aged 3–9 days, 0.087 day⁻¹ ages 10–18, 0.056 day⁻¹ ages 19–29 and 0.019 day⁻¹ for 30 days or more. The mortality rate for fish <3 days old was set equal to that for fish from 3 to 9 days old. Absolute mortality rates most probably differ between the Connecticut and St. Lawrence Rivers, but we assumed that the relative mortality rates between fish of different ages would be similar in the two rivers.

The dip test, a statistical test for discovering the presence of more than one mode in a distribution (Hartigan & Hartigan 1985), was used to test if the distribution of hatching dates observed at any particular sampling date and site differed significantly from unimodal and thus were issued from different spawning events [the dip test was implemented in R (R Development Core Team, 2008)].

Results

The Gompertz growth model relating age to total length of fish whose age was assigned based on otolith microstructure was highly significant ($P < 0.0001$, overall $R^2 = 0.899$; Fig. 3a). The average growth rate over the first 52 days of life (corresponding to the size predicted by the Gompertz growth curve at the age of the oldest juvenile captured) was 1.4 mm per day, as reported in previous studies (Limburg et al. 2003). The growth model was also significant for each of the four groups of fish clustered according to hatch date [22–28 May ($R^2 = 0.675$), 29 May–5 June ($R^2 = 0.902$), 6–19 June ($R^2 = 0.893$) and 20–29 June ($R^2 = 0.833$)] (Fig. 3b). The growth models, however, differed significantly among the four groups (maximum likelihood F -test, $P < 0.0001$). Specifically, parameter b (age at the point of inflection) declined from the earliest through to the latest birth date cluster, with fish hatched between 20–29 June showing a significantly younger age at the point of inflection ($P < 0.01$) relative to all other hatch-date clusters. This is most probably related to water temperature that increased monotonically from 9.5 °C (SE = 0.25) on 2 May to 21.2 °C (SE = 0.28) on 4 July. Nevertheless, juvenile shad hatched earlier in the season always maintained a greater length relative to those hatched later, at least until the end of July (Fig. 4). Growth models developed for each of the three major regions of the river (the upstream region encompassing the

($R^2 = 0.902$), 6–19 June ($R^2 = 0.893$) and 20–29 June ($R^2 = 0.833$)] (Fig. 3b). The growth models, however, differed significantly among the four groups (maximum likelihood F -test, $P < 0.0001$). Specifically, parameter b (age at the point of inflection) declined from the earliest through to the latest birth date cluster, with fish hatched between 20–29 June showing a significantly younger age at the point of inflection ($P < 0.01$) relative to all other hatch-date clusters. This is most probably related to water temperature that increased monotonically from 9.5 °C (SE = 0.25) on 2 May to 21.2 °C (SE = 0.28) on 4 July. Nevertheless, juvenile shad hatched earlier in the season always maintained a greater length relative to those hatched later, at least until the end of July (Fig. 4). Growth models developed for each of the three major regions of the river (the upstream region encompassing the

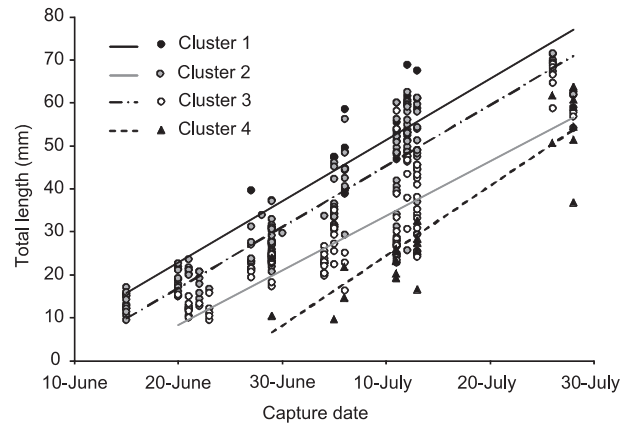


Fig. 4. Total length of juvenile American shad as a function of their capture date for each of the four hatch-date clusters (Cluster 1: 22–28 May; Cluster 2: 29 May–5 June; Cluster 3: 6–19 June; and Cluster 4: 20–29 June), $n = 233$. Straight lines serve to illustrate growth trajectories.

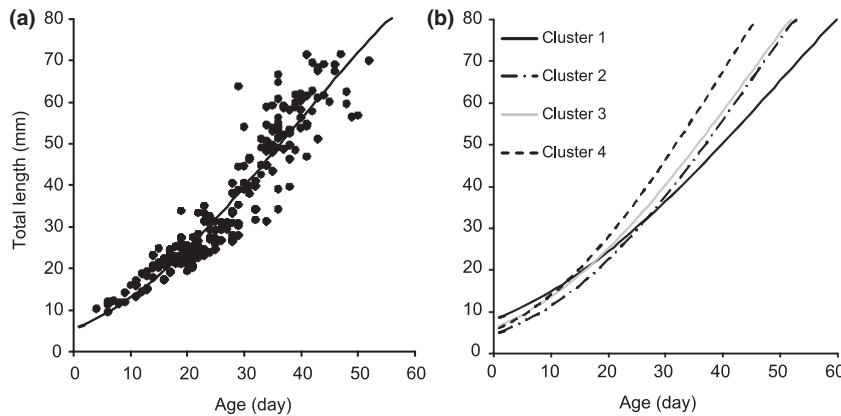


Fig. 3. (a) The Gompertz growth model relating age to total length of fish whose age was assigned based on otolith microstructure ($n = 233$, $P < 0.0001$, $R^2 = 0.899$). (b) The Gompertz growth model for each of the four groups of fish clustered according to hatch date [Cluster 1: 22–28 May ($R^2 = 0.675$); Cluster 2: 29 May–5 June ($R^2 = 0.902$); Cluster 3: 6–19 June ($R^2 = 0.893$); and Cluster 4: 20–29 June ($R^2 = 0.833$)]. The growth models differed significantly among the four groups ($P < 0.0001$).

Montreal and Richelieu sampling sites, the downstream region in the vicinity of Île d'Orléans and the midstream region encompassing the Trois-Rivières and Batiscan sampling sites) did not differ significantly ($P = 0.177$, data not shown).

Hatch-date analysis and duration of spawning

The ages of a total of 2104 fish were available for hatch-date analysis following age assignment. The error associated with the assignment of ages to fish based on size and dates of capture was small. The average estimated age was 29.96 days [SE = 0.68, coefficient of variation (CV) = 2.3%]. Estimates for fish aged from 0 to 10 days were the least precise (CV = 11.8%), whereas all other age groups involved CVs varying from 1.5% to 3.6%.

Hatch dates of all fish sampled throughout the sampling area in June and July 2006 were normally distributed and occurred between 17 May and 5 July (mean = 10 June, SD = 7.61 days). Hatch-date frequency distributions varied according to distance from the river's mouth, with the earliest, latest and mean hatch date occurring increasingly later among fish sampled downstream (Fig. 5).

The weighted regression model applied to examine the hatch-date distribution as a function of the additive effect of site and the date of capture was highly significant ($P < 0.0001$, $R^2 = 0.401$). Isolating the effect of site and date of capture, juvenile shad sampled later in the season exhibited increasingly later hatch dates ($P < 0.0001$, partial $R^2 = 0.287$), as would be expected. However, shad captured downstream were hatched later in the year than shad captured further upstream ($P < 0.0001$, partial $R^2 = 0.114$). Similarly, the weighted regression model applied to examine the age distribution as a function of the additive effect of site and the date of capture was highly significant ($P < 0.0001$, $R^2 = 0.605$). Unsurprisingly, juvenile shad sampled later in the season were increasingly older ($P < 0.0001$, partial $R^2 = 0.530$). However, the spatial signal revealed by the analysis of hatch date was again evident; shad captured downstream were significantly younger than shad captured further upstream ($P < 0.0001$, partial $R^2 = 0.075$).

Additional evidence of multiple spawning events was provided by the multimodal distribution of hatch dates observed during seven discrete sampling events. Significant multimodality in hatch-date frequency distributions were observed on 6 July in the vicinity of the Richelieu R. (FSL-FOIN), on 4 July (S17) and on 10 July at two adjacent stations (N12 and S13) in the Trois-Rivières–Batiscan region and on 20 June (S20), 12 July (N18) and 27 July (N21) in the vicinity of Île d'Orléans (Fig. 6).

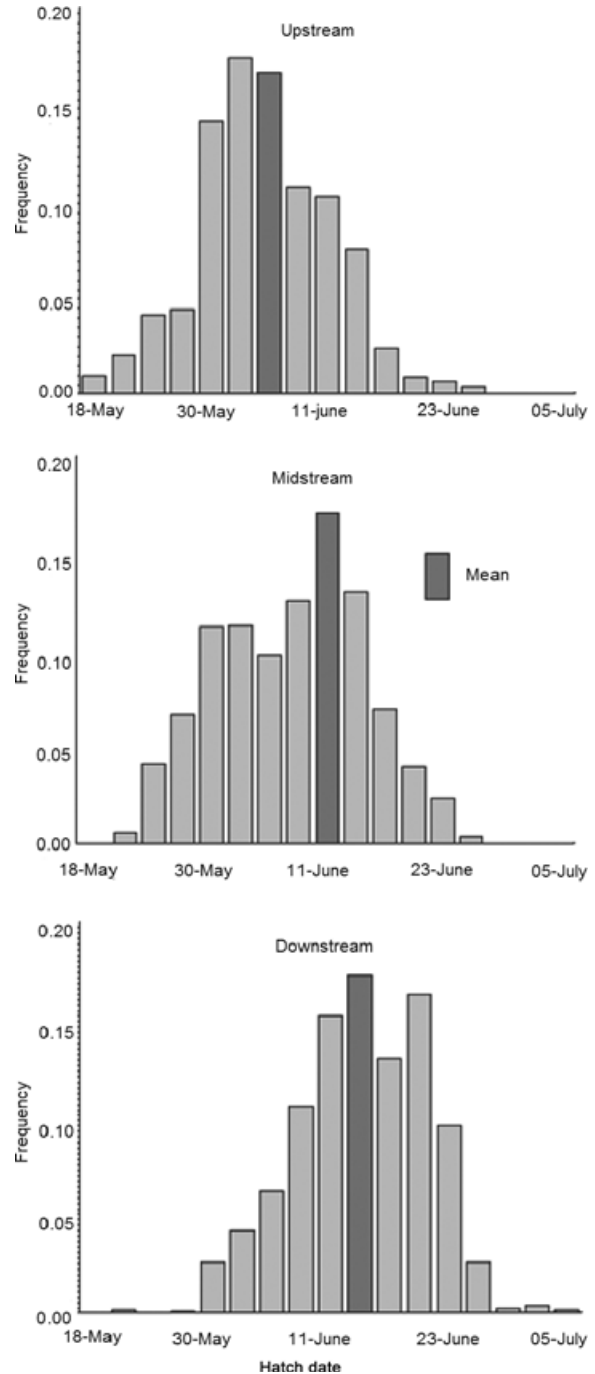


Fig. 5. Frequency distribution of hatch dates in the three major sections of the St. Lawrence R.: Upstream – Montreal and Richelieu R. sampling sites, Midstream – Trois-Rivières–Batiscan sampling sites, Downstream – Île d'Orléans sampling sites. Hatch-date distributions are corrected for differential mortality (see text).

Discussion

Spawning activity of American shad in the St. Lawrence River lasted at least 2 months from early May to early July. Assuming that this spawning activity was limited to the upstream reaches of the

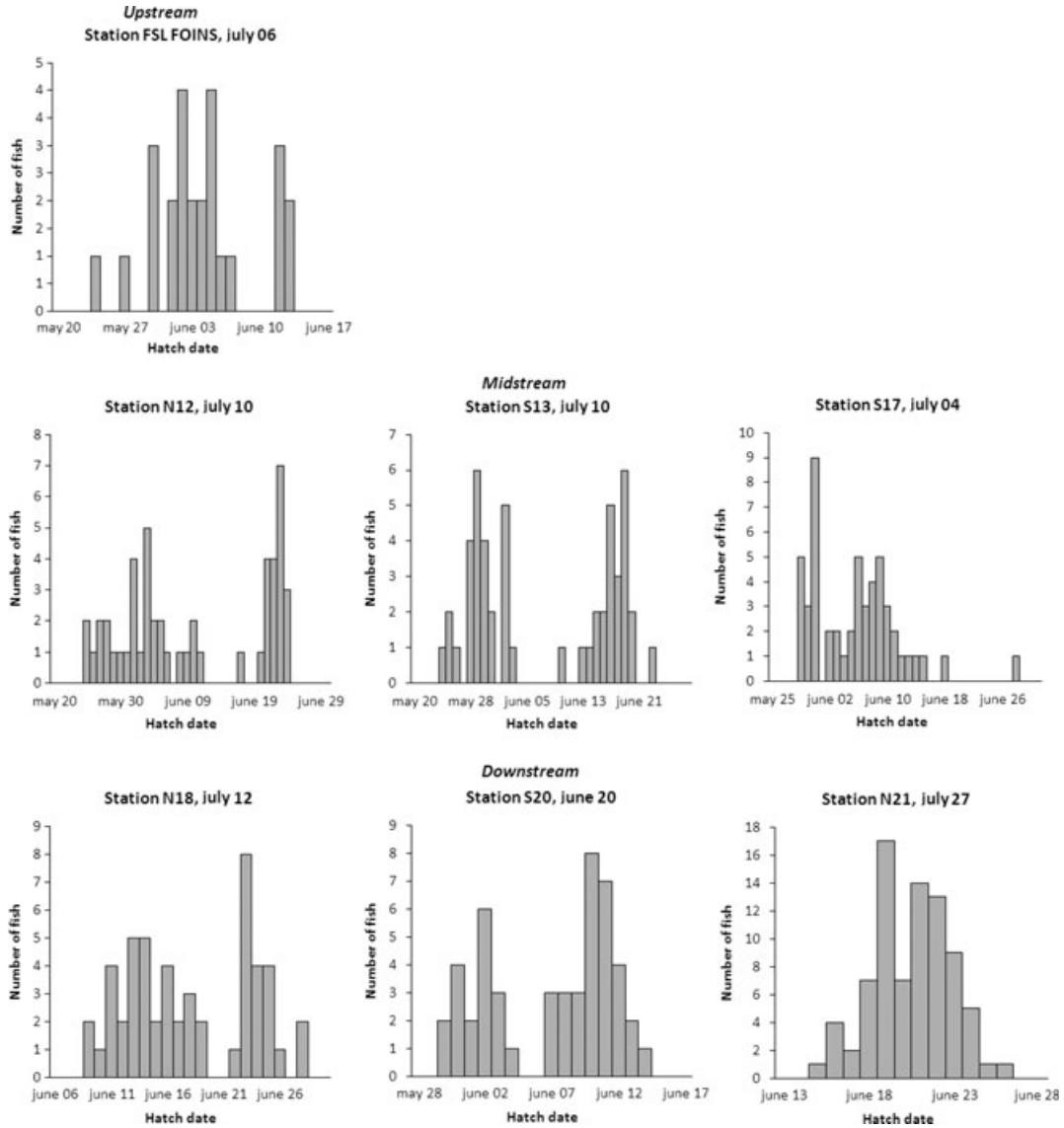


Fig. 6. Distribution of hatch dates at sampling stations that exhibited significant divergence from a unimodal distribution. Upstream (FSL-FOIN, $n = 26$, $P = 0.016$), midstream (N12, $n = 50$, $P < 0.001$; S13, $n = 50$, $P < 0.001$; S17, $n = 52$, $P < 0.001$) and downstream (N18, $n = 52$, $P = 0.002$; S20, $n = 49$, $P = 0.025$; N21, $n = 81$, $P = 0.014$).

St. Lawrence River, we predicted our earliest captures would include larvae hatched in the vicinity of Montreal, with age increasing over time in a downstream direction in concert with the downstream displacement of juveniles. As such, we expected juveniles collected downstream to have hatched earlier in the season than juveniles captured further upstream. We in fact observed the opposite trend. Although considerable overlap in hatch dates occurred along the river, juveniles sampled downstream were hatched later in the season. As a result, younger juveniles were distributed somewhat further downstream. Together with the observation of significant multimodality in hatch-date distributions at midstream and downstream sampling stations, we conclude that the 2-month spawning period involved numerous spawning events

that progressed in a downstream direction as the season advanced, rather than being restricted to upstream sites over the entire spawning period.

This dynamic may have involved batch spawning, whereby individuals migrated to the upstream limit of spawning and then retreated downstream, spawning on multiple occasions as they approached the river's mouth. On the other hand, successive waves of different spawners may have entered the river over the 2-month period, with those adults arriving later migrating shorter distances before spawning as temperatures increased during the spawning period. These two scenarios are not necessarily mutually exclusive tactics. Wild American shad along the U.S. Atlantic coast exhibit group-synchronous ovarian development and individual females spawn repeatedly during each

spawning season (Olney et al. 2001; Olney & McBride 2003). In the York River, ovary size increases as American shad migrate 100 km up the estuary to spawn in freshwater. A spawning cycle of unknown duration involving hydration, ovulation and release of oocytes followed by 1–3 days of no spawning is followed by a repeat in the cycle. Approximately 70% of apparently postspawning fish captured downstream are only partially spent with ovaries that weigh one to eight times those of spent fish (Olney et al. 2001). In addition, approximately one-third of acoustically tagged fish that migrated to spawning grounds in the York River entered both known spawning tributaries before migrating out of the river, although multiple spawning could not be verified (Olney et al. 2006). Within each of the two spawning tributaries of the York River, shad spawn over distances of approximately 50 km (Wilhite et al. 2003). In the case of migrating alewife radio tagged and tracked in the Ipswich River (Massachusetts, USA), bouts of downstream movements following periods of upstream migration were relatively common (Frank et al. 2009). It is not known whether these movements were associated with spawning events. These authors suggested that so-called ‘fallback’ behaviour typically observed in telemetry studies of alosine spawning migrations may not reflect aberrant behaviour but be part of a normal behavioural repertoire. In Allis shad, spawning events have been observed downstream of established spawning grounds in the River Aulne (Brittany) and depending on spawner abundance or environmental conditions, secondary spawning grounds are exploited (Acolas et al. 2004). In this river, migration and spawning activity over time are multimodal and at times appear to involve different spawning sites (Acolas et al. 2006). Together, these observations suggest a large degree of plasticity in alosine spawning dynamics with multiple migration and spawning events spread over time and space. The results presented here are consistent with this scenario.

In conclusion, this study provides evidence that the reproductive activity of the American shad population of the St. Lawrence River involves numerous spawning events that progress in a downstream direction as the season advances, rather than being restricted to known upstream spawning sites. As such, the spawning activity of the shad may not be as compromised as earlier feared. Nevertheless, efforts are needed to identify the location of these new spawning grounds to protect them from any further habitat degradation. This may best be achieved through extensive telemetry studies (e.g., Olney et al. 2006) followed by direct observations of nocturnal spawning activity. A more intensive monitoring of population abundance and reproductive success throughout the river

must be undertaken to assess the population’s ability to sustain itself in the face of future habitat modification.

Acknowledgements

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