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Received: 31 October 2003
Accepted: 8 June 2004
Amended: 28 June 2004

Limnol. Oceanogr., 49(6), 2004, 2310–2315

Synchronized hatch and its ecological significance in rainbow smelt *Osmerus mordax* in St. Mary's Bay, Newfoundland

Abstract—Early life history stages in most marine animals are subject to high mortality through predation, starvation, and dispersal. Accordingly, the potential exists for the selection of behavioral mechanisms that reduce mortality. We examined the ecological significance of synchronization in hatch and the initiation of larval drift in rainbow smelt, *Osmerus mordax*, populations in St. Mary's Bay, Newfoundland. Larval abundances from six 24-h ring net surveys (2-h intervals) in Colinet and Salmonier Rivers during 2002/2003 suggest synchronized hatch following dusk (~2200 h). Monitoring of egg hatching in situ confirmed synchrony was at hatch and not emergence. Larval abundance showed no relationship with temperature or flow rates, and the consistency in hatch pattern suggested a light/dark cue. In experimental manipulations in which eggs were exposed to light and dark conditions for 2-h periods, hatch percentages were up to five times higher ($p < 0.005$) in dark treatments. We hypothesized that the linkage of hatch to low light levels represents a mechanism to avoid elevated larval predation in daylight conditions. Egg predation determined from predator gut content analysis suggested that extreme predation risk from small (<20 cm) salmonids peaked during the day, prior to dusk, and was lowest during night (2200–0400 h). Microcosm experiments demonstrated that newly hatched larvae exposed to predators in dark conditions did not change in number, but mortality averaged 60% in light conditions. Our results suggest that predation pressure during the early life history of aquatic organisms might play a strong role in the optimization of aquatic life histories.

The early life history of many aquatic organisms is characterized by high mortality rates resulting from predation, starvation, and advection from suitable areas (Rumrill 1990; Pepin 1991; Houde 2002). Survival through this period might be determined by the proportion of eggs or larvae that experience favorable conditions (Frank and Leggett 1983; Cushing 1990). Survival and subsequent recruitment could therefore be enhanced if developmental stages could be cued to the timing and location of favorable conditions.

Synchrony and active manipulation of ''developmental events'' has been observed in various taxa, including fishes (e.g., Frank and Leggett 1983), marine invertebrates (e.g., Barry 1989), insects (Dingle 1985), and plants (e.g., Gill 1981; Christensen 1985). These behaviors might dampen the effect of environmental variance and dramatically affect recruitment success and life history evolution (Leggett 1985). However, few attempts have been made to examine how hatch timing contributes to spatial and temporal distribution of aquatic species and the subsequent consequences for survival.

Rainbow smelt, *Osmerus mordax*, display increased nighttime abundance of drifting larvae (Johnston and Cheverie 1988) and appear to synchronize their larval drift from river spawning sites to estuarine habitats further downstream. Throughout eastern North America, smelt time their reproduction to follow the spring thaw, and spawning is characterized by synchronized nightly migrations upstream of the maximum tidal incursion where small (~1 mm) adhesive, demersal eggs are released (McKenzie 1964). Eggs develop in freshwater streams or rivers, and hatch occurs at 10–20 d at 14–16°C. Larvae are then immediately transported downstream to the estuary. Smelt therefore represent a model species for the examination of synchronization and embryological control of hatch. Whether this synchrony in larval drift represents hatch or posthatch emergence from the substrate, how it is cued, and its adaptive significance have not been addressed. We hypothesized that nighttime drift of smelt larvae results from hatch synchrony cued by decreasing light conditions, which is a proxy for decreased predation risk and a ''safe site'' (Frank and Leggett 1982*a*; Bradbury et al. 2000) for hatching larvae. Thus, the objective of this study was to document the process and mechanism of synchronous larval drift in estuarine smelt populations and examine the hypothesis that this behavior represents a response to reduce high predation risk during the early larval period. Specifically, can behavior associated with hatching eggs and larval drift influence subsequent survival?

Methods—Smelt spawning locations were identified through interviews with local residents and subsequent snorkeling surveys during the spring of 2001 in Salmonier and Colinet Rivers, St. Mary's Bay, southeast Newfoundland,

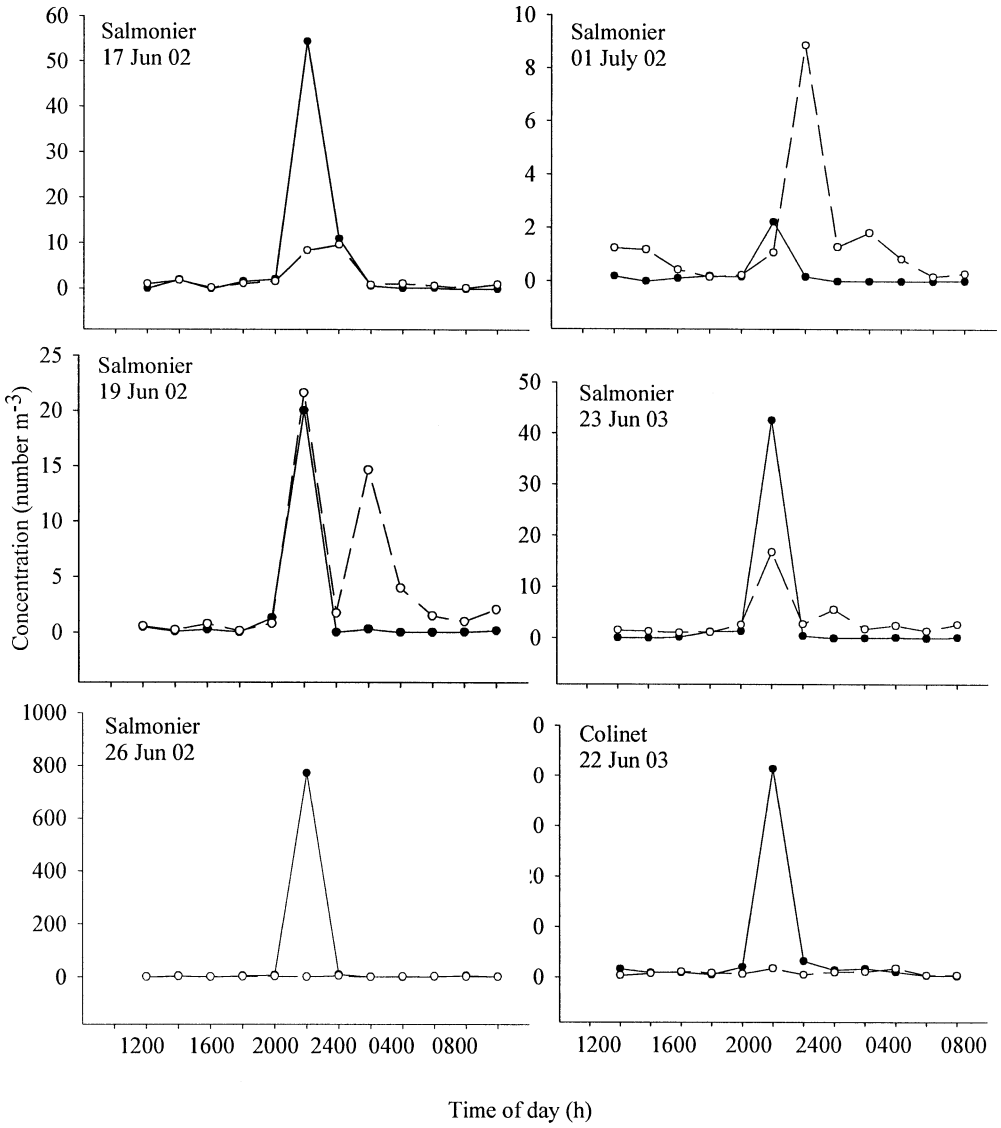

Fig. 1. Temporal distributions of rainbow smelt (*Osmerus mordax*) eggs and larvae in Salmonier and Colinet Rivers during six 24-h sampling series in 2002 and 2003. Solid symbols represent larval concentrations, and open symbols represent egg concentrations.

Canada. Spawning began early in June in 2002 and 2003 and occurred exclusively at night at a location in the rivers just above the tidal influence. During the spawning period, dusk occurred at 2100–2130 h, and nighttime encompassed 2200–0400 h. Within each of the spawning rivers, eggs were deposited over a relatively small bottom area covering 90–100 m^2. Prior to spawning, a portion of the spawning bottom (<50%) was covered with burlap to allow the collection of eggs for further experimentation.

Field collections were made to determine the timing of the initiation of larval drift. Drifting eggs and larvae were sampled ~10 m downstream of the spawning site with a 30-cm ring net with 333-μm Nitex® mesh and fitted with a General Oceanics® flowmeter. Water depth was <1 m, and samples were taken middepth and midstream for a 15-min period at repeated intervals. Ring net samples were taken nightly (at 2200 h) throughout the hatch period beginning in early June to describe seasonality in spawning and hatch patterns. In 2002, four 24-h sampling cycles were completed on Salmonier River with samples taken every 2 h, on 17–18, 19–20, and 26–27 June and on 1–2 July. In 2003, two 24-h sampling cycles were completed: one at Salmonier (23–24 June) and a second at Colinet (22–23 June) Rivers. All 24-h sampling was conducted in conjunction with peaks in seasonal hatch rates on the basis of the nightly surveys. For ring net samples, temperature, and flow speed were determined with an alcohol thermometer and the flowmeter, respectively. All samples were preserved in 95% ethanol. For sample processing, all eggs and larvae were identified to the lowest possible taxonomic level, and abundances exceeding 300 individuals were subsampled with a Motoda splitter.

Larval hatch was monitored in field experiments to separate drift associated with hatch from emergence of larvae from the substrate. Six 10-liter buckets with screened sides (400-μm Nitex, 16-cm^2 windows) were moored in Salmonier River near the spawning site. Eggs were monitored at the

spawning site, and once eggs were near hatch the experiment began. A designation of ''near hatch'' was made through stereoscopic examination of eggs and the observation of beating heart, pigmented eyes, and extensive embryological movement. Burlap subsamples (64 cm^2) were taken from the spawning site and placed into the buckets. Egg distributions on the burlap were uniform, and subsamples from the spawning site were taken within 1 m of each other to ensure similar densities of eggs in each treatment (average 6.7 eggs cm^{-2}). Buckets were monitored, and hatched larvae were removed every 4 h for a 24-h period on 19–20 June 2002. Temperature was monitored in all buckets and was constant, indicating good flow over the burlap.

To investigate the effect of light and dark on hatch, buckets and burlap squares were again used. Nine buckets were set up in groups of three and monitored for 2 h after setup to remove any larvae that hatched as a result of agitation prior to the start of the experiment. Three buckets (1–3) were then covered with multiple layers of black plastic that blocked all light, whereas the remaining buckets were covered with clear plastic. After 2 h, all plastic was removed and hatched larvae were counted and removed. Following an additional 2-h period, the black plastic was moved to three of the buckets that had previously been covered in clear plastic, and the experiment was repeated. The remaining three buckets were maintained as a control for handling effects. This entire procedure was performed on 24 June and repeated with new eggs on 25 June 2003. The numbers hatching in a given treatment were expressed as a percentage of the total hatch for that bucket for that day. All hatch experiments were conducted during peak hatch, which was usually mid to late June.

Predation risk for hatching larvae was evaluated through field collections and gut content analysis of potential predators. First, on 20–21 June a 25-m beach seine was used to sample small (5–20 cm) salmonids schooling near a smelt spawning area in Salmonier River. On 27 June, a 1-m^2 fyke net was placed downstream (~5 m) of a similar spawning site in Colinet River and checked every 6 h from 0400 to 2200 h. This sampling regime was repeated on 28–29 June. In all instances, catches were documented, and small (<20 cm) salmonids were frozen and subsequently sampled for gut content analysis. Given the fast digestion times of larvae in fish stomachs (Folkvord 1993), smelt eggs were used as a proxy for larval predation risk; eggs were present at the spawning site at all times, whereas larvae were largely absent except at 2200 h.

Following the identification of predators, predation risk in light and dark conditions was evaluated with microcosm experiments. To evaluate directly the predation risk for smelt larvae under light and dark conditions, microcosm experiments were carried out on Colinet River. Each microcosm consisted of six Atlantic salmon (*Salmo salar*) parr (5–20 cm standard length) held for 24 h and then placed in a 70-liter plastic container with 600-cm^2 screened sides along with ~1,500 newly hatched larvae (<12 h old) and eggs obtained from the burlap sheets. On 28 June, four microcosms were set up on Colinet River (three with predators and one without) and exposed to natural light from 1600 to 2200 h. Eggs and larvae in each container were then removed and counted. This experiment was repeated on 30 June. Similar experiments were carried out in darkness on 29 and 31 June from 2200 to 0400 h. Numbers of larvae remaining after each treatment were expressed as percent predation loss relative to the control.

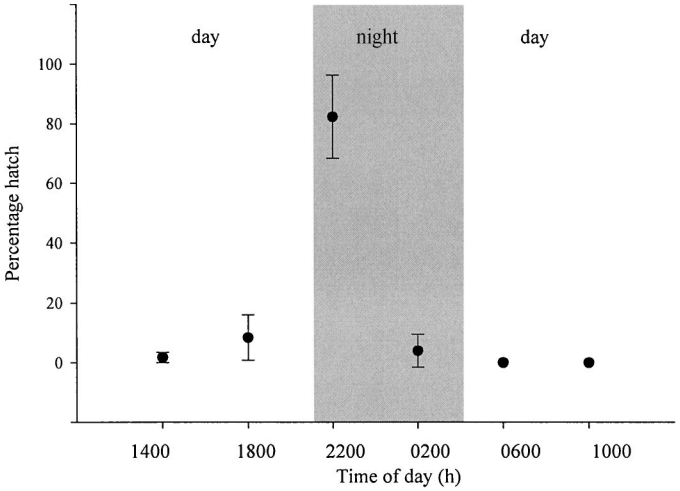

Fig. 2. Percent hatch of rainbow smelt eggs (mean ± SD) monitored in situ for a 24-h period in six screened containers (*see Methods* for description of experimental design).

Results—The 24-h net sampling indicated peak hatch occurred at 2200 h with very low hatch rates at other times (Fig. 1). This pattern was constant throughout the hatch period in Salmonier during 2002 (Fig. 1a–d), in 2003 (Fig. 1e), and in Colinet during 2003 (Fig. 1f). Egg concentrations also peaked during the night, but timing varied between 2200 and 0200 h. There was no relationship between larval concentration and either temperature ($R^2 = 0.02$; $p > 0.1$) or current speed ($R^2 = 0.07$; $p > 0.1$).

The temporal pattern in hatch was also evident in buckets monitored for hatch timing and larval abundance (Fig. 2), in which hatch again peaked around 2200 h and was low at other times of day.

Examination of hatch numbers in response to experimental light and dark treatments showed significant differences (Fig. 3). Hatch percentages in dark treatments averaged 80–100%, whereas hatch in light treatments was 10–20%. This pattern was constant for all experiments regardless of the sequence of light or dark, and 100% of all available eggs had hatched by the end of the experiment. Control treatments that were not exposed to a dark treatment had very low hatch rates in all trials (<5%). Temperatures did not differ among containers.

The fyke and seine nets caught several species of salmonids (5–20 cm standard length) in smelt spawning areas, and no other potential predators were collected in nets or observed in snorkel surveys at the site. The catch contained 23.3% *Salvelinus fontinalis*, 67.4% *S. salar*, and 9.3% *Salmo trutta*. Moreover, fyke nets near the Colinet smelt spawning area indicated that salmonid numbers were lowest during the night and peaked prior to darkness in the 1600–2200 h period (Fig 4a). Gut content analysis indicated all salmonid

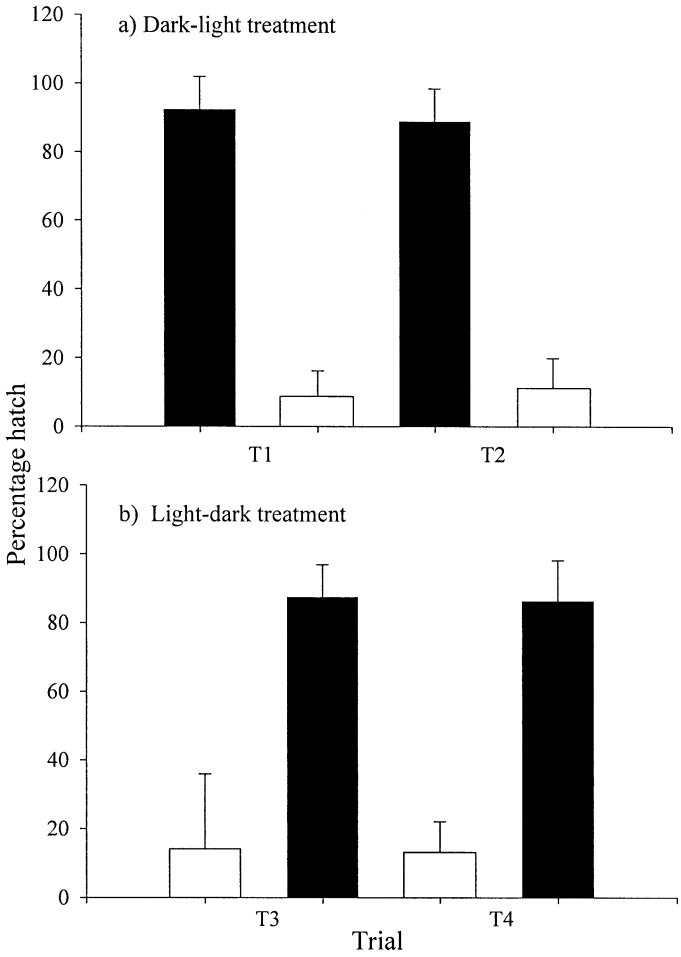

Fig. 3. Hatch (mean ± SD) of rainbow smelt eggs in 5-liter screened containers in Colinet River exposed to light and dark experimental manipulations. Black and white bars represent dark and light treatments, respectively. Each bar represents three replicates involving (a) a dark-to-light treatment or (b) a light-to-dark treatment. See methods in text for further description of experimental design.

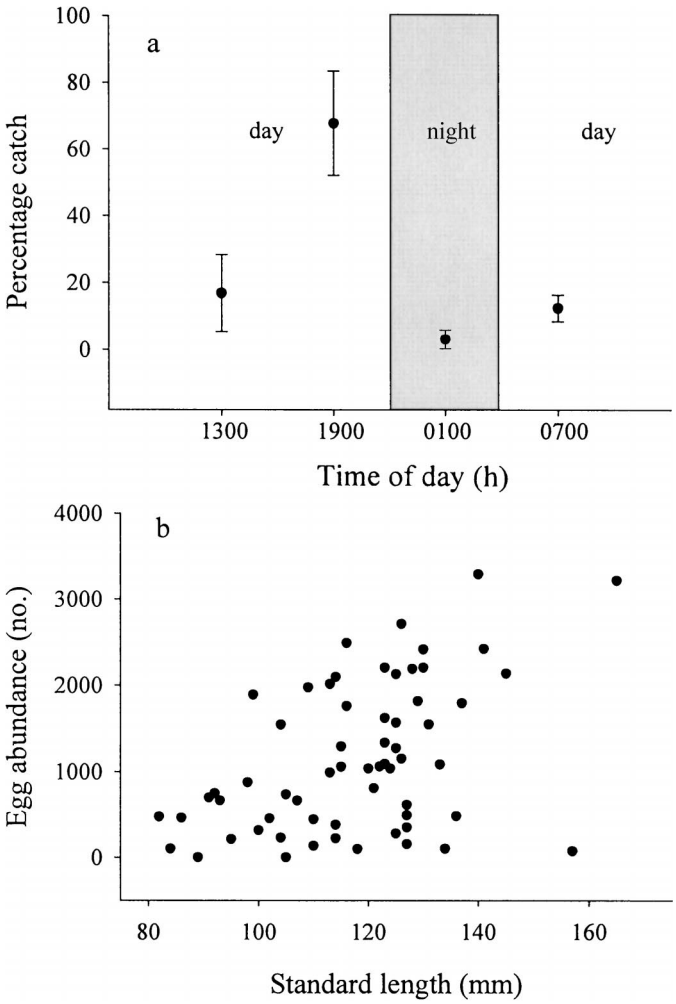

Fig. 4. Predation of smelt eggs by small (<20 cm) salmonids on Salmonier and Colinet Rivers. (a) Predator abundance (mean ± SD) near a Colinet River smelt spawning area over three 24-h periods on the basis of 1-m fyke net catches emptied every 6 h and (b) egg abundances from gut content analysis.

species were active predators on smelt eggs and larvae; salmonid guts contained only smelt eggs and larvae and averaged 1,801 eggs and 3.2 larvae per gut analyzed (Fig 4b).

The microcosm predation experiments confirmed large differences in larval (Fig. 5a) and egg (Fig. 5b) predation between natural light and dark conditions. Larval predation in light ranged from 53% to 64% and was significantly different ($p < 0.005$) from predation in the dark, which averaged 2.6% in both trials (Fig. 5a). Similarly, egg predation rates differed significantly ($p < 0.005$), ranging from 19.9% to 30.4% in light and 2.6% to 7.6% in dark (Fig 5b).

Discussion—The high mortality that occurs during the early life history of many aquatic organisms provides strong selective pressure and might directly influence recruitment dynamics and life history strategies. Our results demonstrate that the synchronization of hatch in coastal smelt populations is cued to low light conditions and conveys survival advantage by exposing larvae to reduced predation levels at night relative to the day. This behavioral pattern supports the hypothesis that predation during the egg and larval period might play a dominant role in the evolution of life history strategies in aquatic organisms.

During the 24-h ring net sampling, a distinct peak in larval abundance was associated with darkness (2200 h). Abundance of eggs also peaked overnight as a result of nighttime spawning behavior, although the actual time varied from night to night between 2200 and 0200 h. Ouellet and Dodson (1985*a*) observed a similar 24-h periodicity in smelt larval concentrations in the St. Lawrence River, peaking at the onset of darkness. Moreover, Johnston and Cheverie (1988) also observed increased nighttime concentrations of smelt eggs and larvae, although larvae peaked between 2200 and 0100 h. The consistency of this pattern over a broad geographic area suggests common predation pressures throughout the range of this species.

The light manipulation experiment and consistency in larval catches suggest that the onset of night cues hatch. Hatch

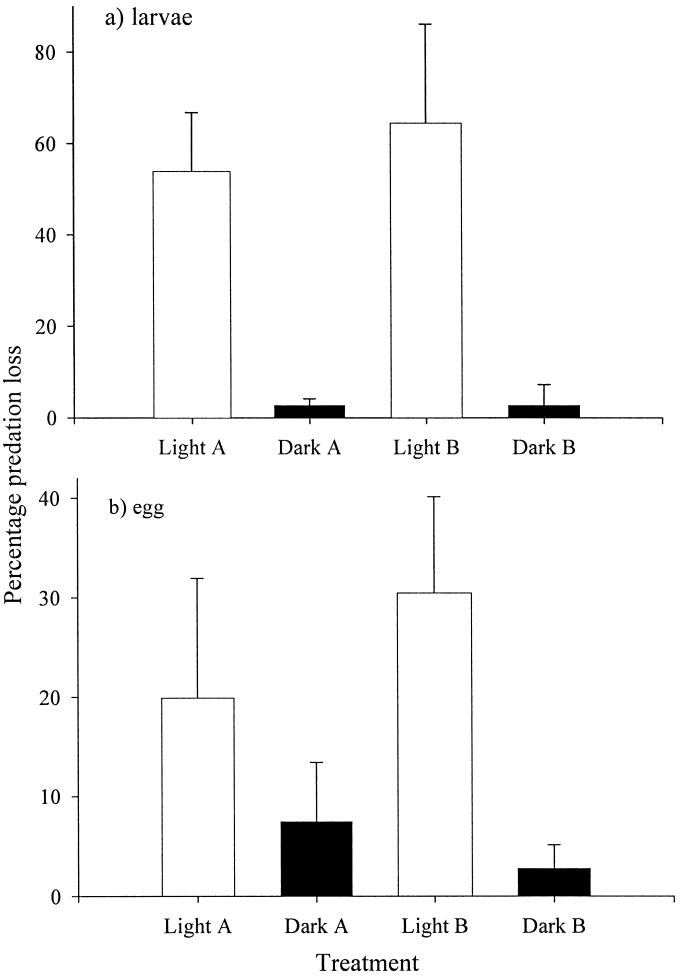

Fig. 5. Predation loss of smelt (a) larvae and (b) eggs in 75-liter screened microcosms in Colinet River. Each contained six small (<15 cm) salmonids and were exposed to 6-h natural light and dark treatments. Bars represent mean and standard deviation of three trials (*see Methods* for description of experimental design).

rates were also similar regardless of whether the treatment sequence was from light to dark or vice versa. Ouellet and Dodson (1985*b*) explored possible cues for synchronized drift and found no relationship between larval abundance and flow rates. They did, however, report a significant correlation between temperature and larval abundance at a 6-h lag, which they suggested might be an artifact of the diel temperature cycle. We observed no relationship between hatch abundance and temperature, and indeed temperature was constant throughout our hatch trials. Hatch was minimal in light treatments, and hatch percentages were small relative to dark treatments, which were often four times greater.

Our observations of predation risk showed a clear diel pattern. Predation risk based on predator abundance at the spawning site was lowest overnight and in early morning and gradually peaked in the afternoon and evening. This pattern coincided with our experimental measurements of larval predation by salmon parr, which also showed increased predation risk in light conditions. However, the predation experiment suggests predation risk is two to three times higher for larvae than for eggs, despite a high egg-to-larvae ratio in gut content analysis, and synchronized hatch could be effective in limiting availability of larvae to predators. Moreover, the nighttime spawning behavior observed in smelt results in peaks in egg concentration during dark and further supports the idea that early life history dynamics might be structured by predators.

Whether the synchronization in hatch is an evolutionary adaptation to reduce larval mortality is uncertain (e.g., Orzack and Sober 2001). We document clear evidence of elevated survival through hatch behavior. Although this time window represents a small component of the larval period, it might encompass a large component of the cumulative mortality, given that measured egg and larval predation rates are significantly higher than those measured for more developed larvae in marine species (e.g., Pepin 1991). The observed synchronization of hatch and resulting elevated larval survival is consistent with increased fitness. Nonetheless, we acknowledge that the heritability and eventual selection pressure on hatch behavior remain to be tested.

The diel pattern in predation risk we observe is consistent with studies on salmonid foraging, which suggest that small salmonids are primarily visual predators and characteristically exhibit diel feeding activity (Hoar 1947; Eriksson and Alanärä 1992). Salmonids are the dominant predator on smelt larvae at hatch at our study site, and hatching at night therefore provides a ''safe site'' for hatching larvae, which can then disperse.

The importance of predation on the early life stages of marine and freshwater fishes has been noted by several authors (Bailey and Houde 1989; Leggett and DeBlois 1994). In marine systems, most research has focused on size selectivity of larval predators (e.g., Pepin and Shears 1995; Houde 1997). Nonetheless, some work has focused on synchronized microscale migration of larvae to increase survival. For example, capelin larvae synchronize emergence from coastal beaches to coincide with wind-induced water mass changes (Frank and Leggett 1982*a*,*b*), which reduces predator abundance and maximizes larval survival.

Here, we provided evidence that synchronized nighttime hatch behavior, which influences spatial and temporal patterns during early life history, might provide a substantial survival advantage as a result of reduced predation pressure. In recent years, interest in larval capacity to regulate spatial pattern has grown significantly, although most studies have focused primarily on late-stage larvae or presettlement juveniles (*see* Bradbury et al. 2003 for an exception). Our study includes prehatch eggs, extending the potential life stages for which active behavior might play a regulatory role and demonstrating broader influences of predation in structuring life history strategies and behavior.

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Received: 15 October 2003
Accepted: 31 May 2004
Amended: 22 July 2004

The authors thank several summer students and local residents of Salmonier and Colinet, Newfoundland, who assisted with this work. L. Barrett, B. Laurel, J. Brown, and P. Pepin assisted and advised on data analysis and interpretation, and two anonymous reviewers provided thoughtful input. IRB was supported by a Natural Sciences and Engineering Research Council (NERC) of Canada Postgraduate Scholarship and a Killam Postgraduate Fellowship.