

Spring migratory synchrony of salmonid, catostomid, and cyprinid fishes in Rivière à la Truite, Québec

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Received April 13, 1983

MONTGOMERY, W. L., S. D. MCCORMICK, R. J. NAIMAN, F. G. WHORISKEY, JR., and G. A. BLACK. 1983. Spring migratory synchrony of salmonid, catostomid, and cyprinid fishes in Rivière à la Truite, Québec. *Can. J. Zool.* **61**: 2495–2502.

During May–June 1980 and June–July 1982, six fish species exited Rivière à la Truite, a major tributary of the lower Moisie River, Quebec, in highly synchronized emigrations. Species included longnose sucker (*Catostomus catostomus*), white sucker (*C. commersoni*), lake chub (*Couesius plumbeus*), juvenile sea lamprey (*Petromyzon marinus*), Atlantic salmon (*Salmo salar*) parr and smolt, and anadromous brook trout (*Salvelinus fontinalis*). In 1980, emigration for all species except the lamprey began on 27 May and ended by 9–11 June; lamprey movements began on 4–5 June and peaked on 10 June. Similar but slightly later patterns occurred in 1982. Onset of the runs in each year coincided with declining water levels and discharge. Thus species of widely different habits exhibit similar and highly synchronized migratory patterns, possibly in response to strong changes in stream environment.

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En mai–juin 1980 et en juin–juillet 1982, six espèces de poissons ont quitté la rivière à la Truite, l'un des principaux tributaires du cours inférieur de la rivière Moisie au Québec, au cours d'émigrations très synchronisées; ce sont: le meunier (*Catostomus catostomus*), le catostome noir (*C. commersoni*), le méné de lac (*Couesius plumbeus*), la lamproie de mer (*Petromyzon marinus*) au stade immature, le saumon de l'Atlantique (*Salmo salar*) aux stades tacon et saumoneau, et l'omble de fontaine (*Salvelinus fontinalis*) anadrome. En 1980, l'émigration de toutes les espèces à l'exception de la lamproie, a commencé le 27 mai pour se terminer vers le 9–11 juin; les mouvements migratoires des lamproies ont commencé le 4–5 juin et ont atteint leur intensité maximale le 10 juin. Les résultats ont été à peu près les mêmes en 1982, mais à une date légèrement ultérieure. Chaque année, le début des migrations a coïncidé avec la chute du niveau et du débit d'eau. Des espèces qui occupent des niches pourtant très différentes ont donc des cycles migratoires bien synchronisés, vraisemblablement en réaction à des changements importants dans le ruisseau.

[Traduit par le journal]

Introduction

Many studies of fish migrations focus on movements of single, often commercially important species, drastic shifts in their habitat, or their travel over long distances (Gauthreaux 1980). We know of no studies that describe synchronous migratory activity for several species of fishes. While conducting a study of anadromous brook trout (*Salvelinus fontinalis*) in the Moisie River system of eastern Quebec (Montgomery et al., in preparation⁴),

we monitored movements of nonsalmonid fishes as well as those of brook trout and Atlantic salmon (*Salmo salar*) in and out of Rivière à la Truite, a major tributary of the lower Moisie River. Four species of nonsalmonids dominated our catch records: sea lamprey (*Petromyzon marinus*), longnose sucker (*Catostomus catostomus*), white sucker (*Catostomus commersoni*), and lake chub (*Couesius plumbeus*). Salmon, brook trout, suckers, and minnows made a simultaneous migration from Rivière à la Truite into the Moisie River. Here we describe that emigration and compare timing and daily catch records for species involved. The results reported here indicate that species of widely different taxa and habits have a similar response to changes in stream environment.

Materials and methods

Sites

The Moisie River is a ninth order stream which empties into the Gulf of St. Lawrence approximately 22 km east of Sept-Iles, Quebec, and about 15 km west of the Woods Hole Oceanographic Institution's Matamek Research Station

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⁴Montgomery, W. L., S. D. McCormick, R. J. Naiman, F. G. Whoriskey, Jr., and G. A. Black. Biology of anadromous brook trout in the Moisie River, Quebec. Manuscript in preparation.

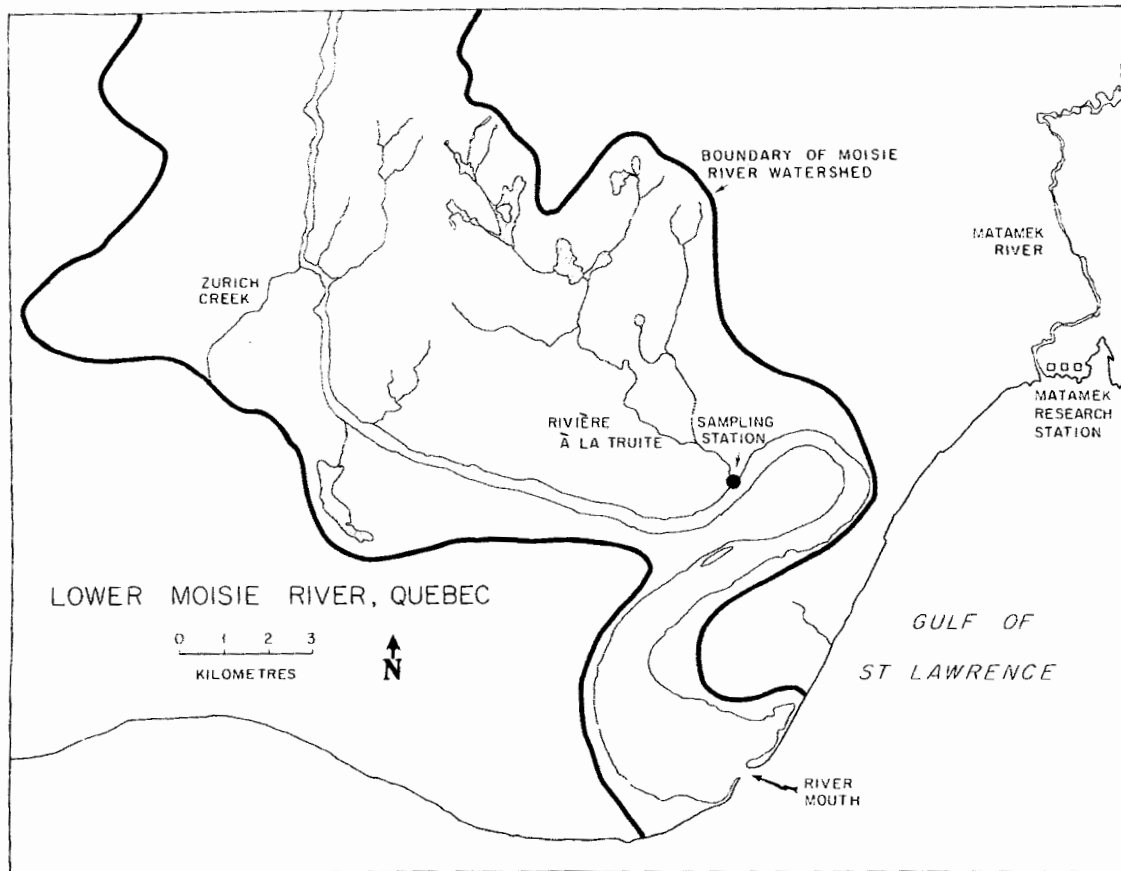


FIG. 1. Map of the north shore of the St. Lawrence River, Quebec, showing the location of the Moisie River and Rivière à la Truite.

(Naiman 1982, 1983). We concentrated our efforts on the major tributary of the lower Moisie River, Rivière à la Truite (Fig. 1).

Rivière à la Truite is a fourth order stream with an average width near its mouth of about 10 m and mean midsummer depth of <math><1\text{ m}</math>. It enters the Moisie River 14 km upstream from the Gulf of St. Lawrence. Rivière à la Truite runs through a spruce-fir boreal forest (*Picea mariana* and *Abies balsamea*), with a riparian zone of speckled alder (*Alnus rugosa*). The substrate is primarily sand and gravel, although some finer sediments reside in pools formed by woody debris. Rivière à la Truite historically supported much larger runs of anadromous brook trout than at present (M. Campbell, Moisie Salmon Club, personal communication), but remains a favored locale for fishermen during the August-September return of these fish.

Sampling procedures

We sampled fish from Rivière à la Truite with hoop nets (1.25-cm stretch mesh). The nets had 1.3-m diameter openings, three conical throats to prevent escape of captured fish, and weighted wings spanning 80-100% of the river's width. In 1980, one net opened upstream to capture fish moving downstream, while an adjacent net opened downstream to

capture fish moving upstream. These nets were monitored from 19 May to 11 November. In 1982 two nets placed 20 m and 100 m from the mouth of Rivière à la Truite were operated between 29 May and 5 September. The net closest to the river mouth experienced higher and more variable water depths, and more variable catch data. When water levels dropped (July 15) this net was reversed to catch incoming brook trout for a related study. Detailed catch data for 1982 are presented only from the upstream net which was set nearest the locations of 1980 nets. Water depths were measured from stakes driven into the riverbed or hung from trees along the riverbank; water temperatures were measured using maximum-minimum thermometers placed at depths $\geq 1\text{ m}$.

During the peak periods of migration in 1980 and throughout the sampling period in 1982, nets were monitored daily. After migration subsided in 1980, nets were monitored every 2nd or 3rd day. All captured fish were removed to holding pens near shore. Lamprey were counted but not measured. We anesthetized all other fishes with MS-222 (tricaine methane sulfonate) or phenoxyethanol, measured fork length to the nearest millimetre, weighed salmonids to 0.1 g, and returned specimens to holding pens for recovery. In 1982 all captured fish except lamprey were fin clipped (a triangular notch in caudal or pelvic fin) prior to release. Fish

were not fin clipped in 1980. Fully recovered individuals were placed downstream of the net where they were captured if they were moving downstream and upstream of the net if they were moving upstream.

Nets were checked at about the same time each day, and procedures for sampling and resetting nets were consistent. Because shore attachments of net wings remained undisturbed throughout check and reset, position of the nets in the stream did not change from day to day except on two occasions in 1982.

Results

Net efficiency

To interpret daily catches as real indicators of the number of fish moving, it is necessary to know if net efficiency remained constant. Daily recapture rates (percentage of daily catch with fin clips) and total recapture rate (percentage total yearly catch with fin clips) of each species except lamprey were calculated for the 1982 catch between May 28 and June 28. Recaptures result when fish released downstream of the net in which they were first captured swim upstream (over the net) and then return downstream and are recaptured. Total recapture rates during this period for each species were the following: brook trout, 2.7%; salmon, 0.6%; longnose sucker, 14.2%; white sucker, 13.1%; and lake chub, 6.1%.

Although daily recapture rate is not a true measurement of net efficiency because of differences in immigration and emigration rates, it can give an indication of short-term variations in catch efficiencies. We have tested two hypotheses relating to the role of net efficiency in determining total daily catch. The first involves the degree of correlation between the percentage of marked fish recaptured and the total catch. If variations in net efficiency were primarily responsible for capture levels, peaks in capture should have higher recapture rates. (This will not be true if the available number of marked fish is small. However, the large number of captures on days just prior to the day of peak capture provide a large number of marked fish whose recapture rate is unlikely to go down at the same time that net efficiency goes up.) For brook trout, salmon, and lake chub, days of peak capture had recapture rates that were less than the total recapture rate for that species. Recapture rates on the day of peak migration for white and longnose sucker were higher than total recapture rate with no statistical significance for white sucker ($p = 0.94$) and possible significance in longnose sucker ($p = 0.07$, arc sine transformation of percentages, Sokal and Rohlf 1969, p. 610). Daily recapture rate regressed on total daily capture of each species could only explain between 1.0 and 11.3% of the variation in total daily capture (brook trout, $r^2 < 0.01$; salmon, $r^2 = 0.08$; longnose sucker, $r^2 = 0.11$; white sucker, $r^2 = 0.01$; lake chub, $r^2 < 0.01$).

The second test of changes in net efficiency is the degree of correlation between species catches over short time intervals. In 1980 the daily catches of trout and salmon rose throughout the major portion of the run, in contrast to the decline of sucker and chub. For net efficiency to account for this pattern, recapture rates for the species groups would have to change in opposite directions over very short time periods. This is not only counterintuitive but receives no support from our 1982 recapture rate studies. Neither patterns nor differences in total catch can be easily ascribed to sampling procedures or efficiency of net function. Therefore we interpret our daily catch statistics as representing real variations in the number of daily migrants.

Fish movements

General aspects

Two major migrations occurred at Rivière à la Truite in 1980. Six fish species (sea lamprey, Atlantic salmon, brook trout, longnose sucker, white sucker, lake chub) emigrated from the river, five of them in temporal synchrony during late May to early June (Fig. 2a). Activity in the river remained low thereafter until early August to early September. At this time there was an immigration of brook trout, the second case of migratory activity. We detected no movements of suckers or chubs back into Rivière à la Truite but did record a small influx of adult lamprey during the August–September brook trout immigration; lamprey were observed spawning in the river during this latter period (J. Gustin, personal communication).

In 1982, the emigration began in early June and again involved brook trout, Atlantic salmon parr, longnose and white suckers, lake chub, and sea lamprey (Fig. 2b). There was generally greater day to day variation in catches of all species during 1982 than in 1980. This may relate to a more variable discharge due to heavy sporadic rains in 1982 (Figs. 3a, 3b), but may also partially derive from changes in net position. On 15 and 23 June the net was moved after destruction of its attachment sites. Peaks appeared for all species except the lamprey on 16 June, and a similar pattern obtained for all except white sucker on 25–26 June. Nonetheless, variation in daily catch remained high following the final (23 June) change in net position (Fig. 2b). The 1982 emigration was protracted over a 30- to 40-day period compared with an approximately 15-day period in 1980; river depth took 2 months to drop from its annual maximum to midsummer low levels during 1982, but only one month in 1980. Otherwise, dynamics of the spring migration were similar in both years; significant teleost migration did not begin until 6–8 days after peak high water. In each year a full moon occurred within 4–7 days after peak high water, so that we could not evaluate the relative importance of these two factors in

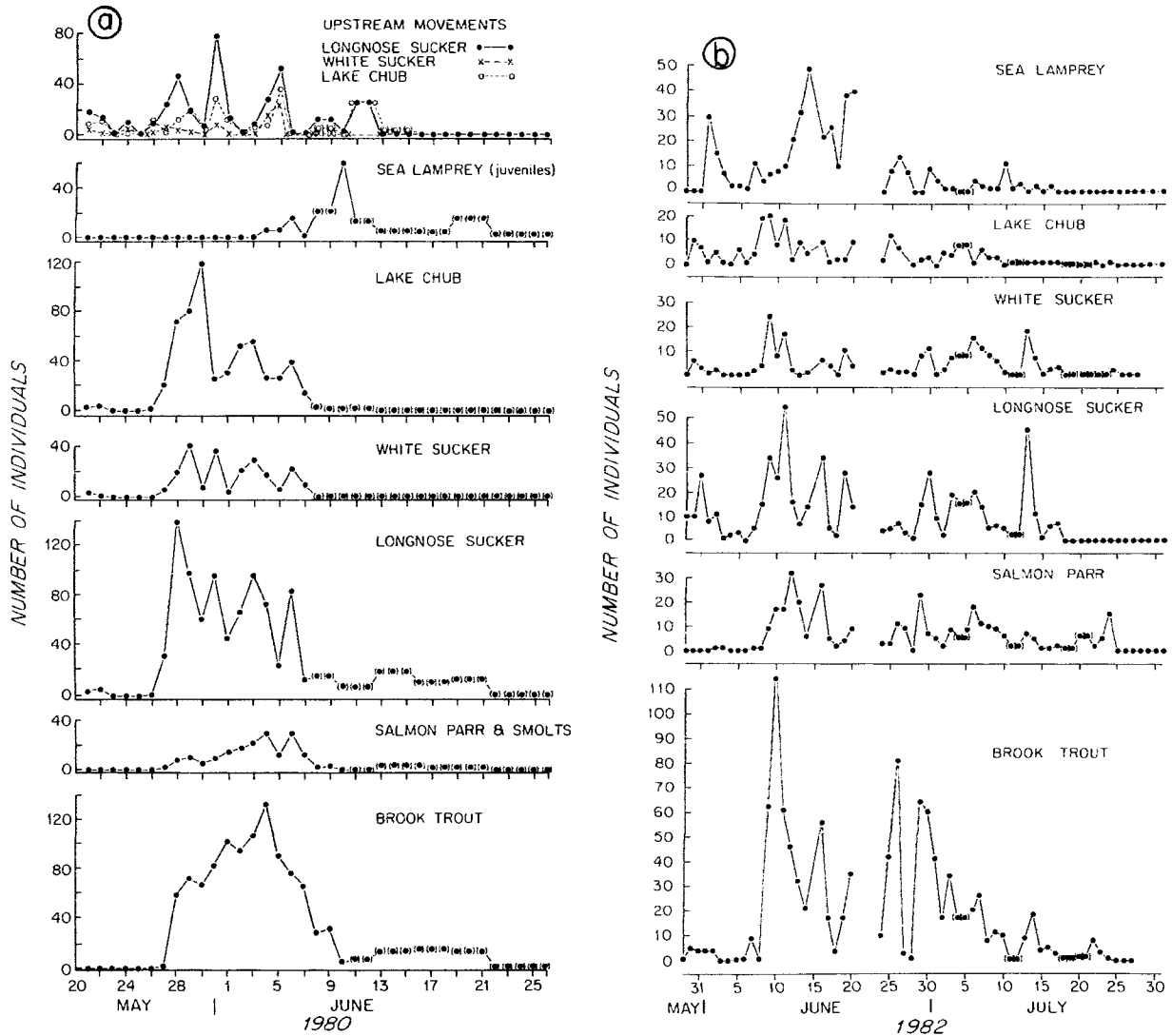


FIG. 2. Daily captures of fishes in Rivière à la Truite during 1980 (a) and 1982 (b). Top panel for 1980 is a composite plot of cyprinids taken moving upstream. All other graphs are captures of fish moving downstream. Points in parentheses are average daily catches for periods when nets were checked at greater than daily intervals.

stimulating migration. The regular, multiple peaks in emigration of longnose sucker, white sucker, and lake chub in 1980 make lunar periodicity an unlikely environmental cue for these species, at least as a regulator of activity during the run.

Longnose sucker (*Catostomus catostomus*)

In 1980, captures of longnose sucker moving downstream ranged from 0 to 5 individuals per day in the 6 days prior to 27 May, but on 27 and 28 May we recorded 30 and 140 specimens, respectively (Fig. 2a). The numbers of fish moving upstream were generally fewer than those moving downstream. The run declined

rapidly after 7 June; of the 1096 specimens captured in the 35 days from 21 May to 26 June 1980, 74.5% were taken in the 12 days from 27 May to 7 June. Length-frequency distributions for longnose sucker moving upstream and downstream in 1980 (Fig. 4) suggest that a relatively larger fraction of upstream migrants were small fish than was the case for downstream migrants, but those distributions were not significantly different by the Kolmogorov-Smirnov test ($p > 0.2$; Zar 1974). Two size classes of fish are evident, with modes at 120–130 and 210–220 mm. We did not attempt to age specimens but work at the site by M. Zalewski in 1981 (personal communication) makes it

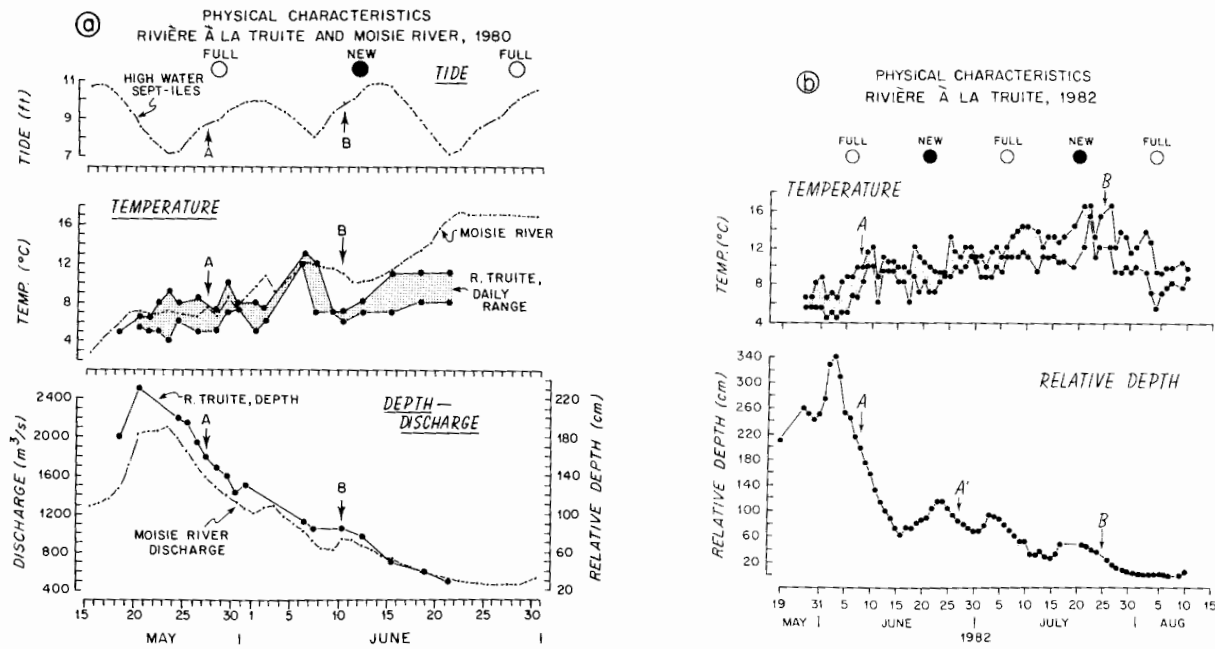


FIG. 3. Physical characteristics of Rivière à la Truite and the Moisie River during May–June 1980 (a) and May–July 1982 (b). In each graph, arrow A designates the onset of emigration from Rivière à la Truite, while arrow B indicates the end of the teleost emigration. (1 ft = 0.3048 m.) A' marks the onset of a second period of apparent migratory activity following a change in net position on 23 June.

clear these modes did not represent discrete age groups, so their significance remains uncertain. Forty-three sacrificed specimens, ranging from 55 to 252 mm fork length (FL), included 6 mature females (95–195 mm), 16 immature males (64–184 mm), 7 mature males with breeding tubercles (177–224 mm), and 12 of undetermined sex (62–114 mm). A regression of length (L , in millimetres) on weight (W , in grams) from these specimens yielded $\log_{10}(W) = 3.01 \log_{10}(L) - 5.02$ ($r > 0.99$). Using this relationship, we generated a weight estimate for each individual moving downstream in Rivière à la Truite during 1980 and by summation produced a minimal estimate of the biomass of longnose sucker leaving the river: 92.1 kg.

Early emigration of longnose sucker, white sucker, and chub in 1982 may have been missed, since some catches were made on the first sampling day. A minor peak of longnose sucker (27 individuals) occurred on 31 May, prior to the initiation of the major exodus (Fig. 2b). Catches then declined to 0 on 6 June, after which they increased to 34, 26, and 54 on 9, 10, and 11 June, respectively. The migration ended by 18 July. We captured only 43.2% of the total sample in the 12 days after onset of the 1982 migration, in contrast to 74.5% for the same time period in 1980.

White sucker (*Catostomus commersoni*)

The rapid rise to the peak daily captures of white

sucker commenced on 27 May 1980 (Fig. 2a). Fish moving upstream were generally outnumbered by those moving downstream. Of fish captured moving downstream, 227 (93.8%) were taken between 27 May and 7 June 1980. There is no statistical difference in the length–frequency distributions of fish moving upstream versus downstream, and no distinct size modes are evident (Fig. 4).

Seventeen specimens ranging from 62 to 399 mm FL formed the basis for the length–weight regression: $\log_{10}(W) = 3.14 \log_{10}(L) - 5.25$ ($r > 0.99$). All specimens ≥ 260 mm were mature (both males and females), and all ≤ 150 mm were immature; we sacrificed no specimens between 150 and 260 mm. The minimum biomass of white suckers exiting Rivière à la Truite in 1980 was 79.5 kg.

From 29 May to 8 June 1982, captures of white suckers ranged from 0 to 6 ($\bar{x} = 1.4$), rising to 24 on 9 June (Fig. 2b). We captured only 37.0% of the total sample ($N = 216$) in the 12 days from 8 to 20 June; in 1980, 93.8% of the sample was taken in a similar period.

Lake chub (*Couesius plumbeus*)

The pattern produced by downstream movement of lake chub in 1980 was similar to that for both species of sucker (Fig. 2a). The chub exodus began on 27 May and was virtually complete by 8–9 June. Of the 580 specimens captured in May and June, 95.3% were taken in the 27 May – 7 June period.

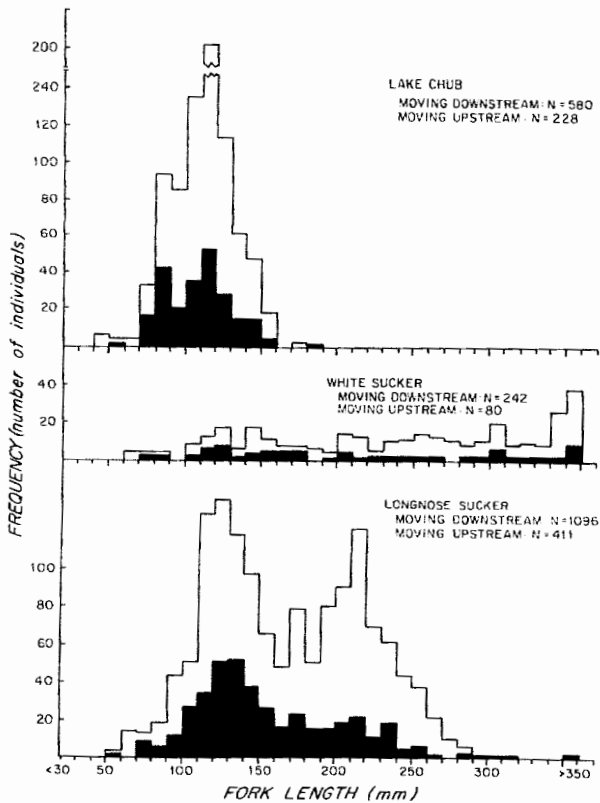


FIG. 4. Length-frequency distributions for fishes moving upstream and downstream in Rivière à la Truite, May-June 1980. Open portions of bars give numbers moving downstreams; solid portions tally fish moving upstream. Bar height totals all captures.

Length-frequency distributions of upstream versus downstream moving fish (Fig. 4) are statistically indistinguishable, and no clear size modes are discernible. Twenty seven specimens (73–145 mm FL) generated a length-weight regression of $\log_{10}(W) = 3.24 \log_{10}(L) - 5.45$ ($r > 0.99$). Mature females covered the entire size range of our sample. The minimum biomass of lake chub departing the river in May-June was 13.5 kg.

In 1982 the major emigration peak coincided with peaks for the salmonids and catostomids (Fig. 2b) but was less marked than in 1980. The rise to that peak began on 7 June. Only 49.3% of the total sample of 211 fish was captured during the 12 days following onset of the major emigration.

Brook trout (*Salvelinus fontinalis*)

Brook trout captures rose from a single fish on 27 May 1980, the initial day of activity for other teleosts, to 58 fish on 28 May (Fig. 2a). In contrast to the general pattern for sucker and chub, catches rose rather steadily to a single distinct peak of 132 fish on 4 June, before declining rapidly.

During May and June, 1097 brook trout were captured moving downstream and only 39 moving upstream. Details of these movements will be presented elsewhere as part of a larger study on anadromous trout (Montgomery et al., see footnote 4), but analysis of length-frequency distributions demonstrate that fish moving downstream tend to be larger than those moving back into the river during the same period ($p < 0.01$, Kolmogorov-Smirnov test). Regression of length on weight of emigrants for which we had both length and weight data gave $\log_{10}(W) = 2.62 \log_{10}(L) - 3.26$ ($r = 0.97$, $N = 825$). Our minimum biomass estimate for trout leaving the river is 39.5 kg.

As in 1980, brook trout in 1982 exhibited the most pronounced peak in captures, rising from 0 to 9 fish per day prior to 9 June to 114 fish on 10 June (Fig. 2b). While the 1980 run was virtually complete in the two weeks between 27 May and 10 June, the 1982 emigration ($N = 1011$) spanned approximately 5 weeks (8 June to about 15 July).

Atlantic salmon (*Salmo salar*)

Of the 216 salmon parr and smolt captured moving downstream in May and June, 84.7% departed between 27 May and 12 June 1980 (Fig. 2a). We netted no salmon prior to 27 May; daily catches rose until 4-6 June and then fell rapidly to zero. Only 23.8% of the departing fish were identifiable as smolts or potential smolts, so that the emigration was dominated by size and age classes normally not considered migratory. Based on mean fork length and weight for all specimens, a minimum estimate of salmon biomass leaving the river was 3.7 kg.

During 1982 salmon parr, like trout, showed a strong surge of migratory activity that began on 9 June and reached a peak on 12 June (Fig. 2b). Only 44.1% of the total sample ($N = 345$) were captured in the first 18 days of sampling, roughly one-half the proportion captured in a similar period during 1980.

Sea lamprey (*Petromyzon marinus*)

The lamprey migration differs markedly from those of the other fishes. The run is clearly dominated by juveniles moving downstream; we captured 309 juveniles moving downstream and 2 moving upstream in 1980 (Fig. 2a). Only 11 adults entered either of our nets during May-June. The run did not begin until 4-5 June, at a time when teleosts had virtually completed their departure, and it extended over at least 3 weeks. We collected no detailed information on sizes or weights of lampreys and attempted no biomass estimates, but measurements of preserved specimens indicated that juveniles averaged approximately 130 mm total length and 3-4 g.

In accord with 1980, the 1982 lamprey migration came after the departure of the teleosts (Fig. 2b). This was true for the teleost movements of 30 May - 2 June

TABLE 1. Smirnov test statistics (D) for all two-way comparisons of 1982 cumulative catch frequency distributions. Results demonstrate that lamprey migration pattern differs from all teleosts, except perhaps lake chub. Lake chub migratory pattern differs from white sucker and salmon parr. D = maximum d_i , where d_i is the difference between the observed cumulative frequencies, i = sample day, and n = total sample size. Critical values were calculated following Conover (1971, p. 399). BT, brook trout; P, salmon parr; LN, longnose sucker; WS, white sucker; LC, lake chub; and SL, sea lamprey

| | BT | P | LN | WS | LC | SL |
|----|----|------|------|------|--------|--------|
| BT | — | 0.19 | 0.13 | 0.25 | 0.26 | 0.33* |
| P | — | — | 0.22 | 0.17 | 0.34** | 0.38** |
| LN | — | — | — | 0.14 | 0.18 | 0.30* |
| WS | — | — | — | — | 0.32* | 0.44** |
| LS | — | — | — | — | — | 0.24 |
| SL | — | — | — | — | — | — |

* $P < 0.05$.

** $P < 0.01$.

and 8–11 June, which were followed by lamprey movements on 1–3 June and 12–15 June, respectively. The cumulative frequency distribution for catches of lampreys differed significantly ($p < 0.05$, Smirnov test, $N = 47$ days compared, Table 1) from distributions for all teleosts except lake chub, supporting the contention that lamprey movements were quite different than those of other fishes.

Discussion

Salmonid, catostomid, and cyprinid fishes of Rivière à la Truite exit the river during an explosive, downstream migration beginning in late May or early June. In 1980 that mass movement began on 27 May for all three cyprinoids and perhaps salmon, and on 28 May for brook trout. The run of all species was largely complete by 10 June. By 10 June 1980, we had captured 2777 sucker, chub, salmon and trout moving downstream. Sucker and chub alone accounted for a loss of approximately 185 kg of fish from the river, while trout and salmon made up an additional 50 kg. We emphasize that these numbers are probably severe under-estimates, because during the peak portions of the runs we were fishing with fyke nets 1.3 m in diameter in a river that was 2 m or more in depth. Estimates of net efficiencies in 1982 indicate that we may have captured as few as 1–14% of the emigrants, depending on the species.

We know of no other reports of interspecifically synchronous, migratory movements among fishes. Most studies report seasonal movement patterns of single species (Storck and Momot 1981; Werner 1979; review in Hall 1972; Gauthreaux 1980), and those that treat multiple species (Gerking 1950, 1959; Funk 1955; Hall 1972) do not deal with possible interspecific relationships. Our data differ from previous studies in

following movements of multiple species on a daily basis. This allowed us to identify the explosive onset of emigration as well as two patterns which may reflect ecological or behavioral interactions between species: synchrony among teleosts and lamprey asynchrony with teleosts.

We have no explanation for the timing of departure of juvenile lampreys, which was initiated in both 1980 and 1982 after the runs of other species had subsided. This unique pattern of lamprey movement indicates either a differential response of this species to changes in stream environment or other environmental cues for migratory activity. Movements in 1980 followed a period of increasing water temperatures, and a similar increase preceded the major emigration in 1982. Adult brook lamprey (*Lampetra planeri*) cue on water temperature in other systems (Malmqvist 1980). However, an earlier peak of activity (1 June 1982) was not preceded by a period of rising temperature in our study. The adaptive significance of lamprey movements may relate to the movements of the other fishes. It is conceivable that benefits might accrue through allowing major predators to leave the stream system and be diluted in the larger river, or from having potential hosts preceding them into the river and the sea.

Given the synchronous form of the movements of the remaining five species of fishes from the river (Figs. 2a, 2b), cues should be sought that initiate these movements. There was no clear relationship between water temperature and the onset of migration in either year, although a period of possible temperature increases preceded the 1982 migration. Migration in both years began 4–7 days after peak high water. The weather was consistently clear and sunny during the migration period in 1980, but was clear to cloudy and rainy in 1982. Spring tides in the Gulf of St. Lawrence do produce detectable changes in water levels at the mouth of Rivière à la Truite, but tidal ranges at the time of the run in 1980 were small compared with those in mid-May and were not noticed upstream in Rivière à la Truite.

In both sample years, the mass movements occurred during periods of dropping water levels shortly after peaks in spring runoff; these or correlated events may have stimulated the run, but the apparent synchrony of the run between such taxonomically and ecologically diverse species suggests other factors may play an important role. One such factor may be inter- and intra-specific social interactions resulting from migratory restlessness or migratory movements of one species, akin to the "Zugunruhe" described for birds (Emlen 1972). To our knowledge, agonism between fishes during migratory periods has not received extensive study, but the likelihood of encounters must increase during times of mass migrations and dropping water levels.

Acknowledgements

Research support was provided by the Matamek Research Program of Woods Hole Oceanographic Institution; W. L. Montgomery was supported by a Woods Hole Oceanographic Institution Postdoctoral Scholar Fellowship and S. D. McCormick was supported by a Tai-Ping Predoctoral Fellowship in Marine Biology, funded by the Tai-Ping Foundation. We thank Matamek Research Station personnel, particularly Ellyn Montgomery, for field assistance and Elaine M. Lynch and Dianne Steele for typing the manuscript. Dr. Michael Healy made substantial improvements to the manuscript. Contribution No. 5153 of the Woods Hole Oceanographic Institution and Contribution No. 73 of the Matamek Research Station.

- CONOVER, W. J. 1971. Practical nonparametric statistics. John Wiley & Sons, New York.
- EMLEN, S. T. 1972. The ontogenetic development of orientation capabilities. Animal orientation and navigation. NASA (Spec. Publ.) SP-262. pp. 191-209.
- FUNK, J. L. 1955. Movement of stream fishes in Missouri. Trans. Am. Fish. Soc. **85**: 39-57.

- GAUTHREAUX, S. A., JR. (Editor). 1980. Animal migration, orientation, and navigation. Academic Press, New York.
- GERKING, S. D. 1950. Stability of a stream fish population. J. Wildl. Manage. **14**: 193-202.
- . 1959. The restricted movement of fish populations. Biol. Rev. **34**: 221-242.
- HALL, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology, **53**: 585-604.
- MALMQVIST, B. 1980. The spawning migration of the brook lamprey, *Lampetra planeri* Bloch, in a South Swedish stream. J. Fish Biol. **16**: 105-114.
- NAIMAN, R. J. 1982. Characteristics of sediment and organic carbon export from pristine boreal forest watersheds. Can. J. Fish. Aquat. Sci. **39**: 1699-1718.
- . 1983. The annual pattern and spatial distribution of aquatic oxygen metabolism in large boreal forest watersheds. Ecol. Monogr. **53**: 73-94.
- SOKAL, R. R., and F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, CA.
- STORCK, T., and W. T. MOMOT. 1981. Movements of the creek chub in a small Ohio stream. Ohio J. Sci. **81**: 9-13.
- WERNER, R. G. 1979. Homing mechanism of spawning white suckers in Wolf Lake, New York. N.Y. Fish Game J. **26**: 48-58.
- ZAR, J. H. 1964. Biostatistical analysis. Prentice Hall, Englewood Cliffs, NJ.