International Council for
the Exploration of the Sea

C.M. 1977/M:17
Anadromous and Catadromous
Fish Committee

DOWN-ESTUARY MIGRATION OF HATCHERY-REARED ATLANTIC SALMON (*SALMO SALAR*) SMOLTS, AND ITS RELATION TO TIDAL CURRENTS

by

James D. McCleave

Migratory Fish Research Institute
and Department of Zoology
University of Maine
Orono, Maine 04473 USA

ABSTRACT

The objectives of this study were to determine by ultrasonic telemetry factors influencing initiation of migration of hatchery-reared Atlantic salmon smolts, routes and rates of down-estuary travel and influence of water currents on migration. Forty-six smolts were tracked. Early in spring smolts were quite inactive. After water temperatures exceeded 9° C nearly all smolts moved quickly away from the release point and made substantial seaward progress. Most smolts moved in main channels, away from shore, and near the surface. Overall mean ground speed was about 40 cm s^{-1} (1.7 body lengths s^{-1}), but depended on tidal current speed. Migration through the estuary is largely due to passive drift on the rapid tidal currents.

INTRODUCTION

Anadromous Atlantic salmon, <u>Salmo</u> <u>salar</u>, once an abundant New England food and game fish, has been eliminated from all its native rivers of the U.S.A. east coast except for a few Maine rivers which support small populations. The Penobscot River, Maine's largest, was designated a model for salmon restoration (Everhart and Cutting 1967), and in 1977 over 340,000 smolts were stocked into the river at head-tide and upriver locations.

Recent studies have contributed to understanding of the freshwater portions of the seaward migration of smolts (e.g. Bakshtansky et al. 1976, Bartel 1976, Jessop 1975, Solomon 1975, Stasko et al. 1973). There are few observations of smolts in estuaries and these are largely anecdotal (Calderwood 1908, Huntsman 1962, Stasko et al. 1973), though Calderwood (1908) presented some evidence for a rapid passage through the estuary.

Objectives of this study were to determine for hatchery-reared Atlantic salmon smolts in the Penobscot Estuary by ultrasonic telemetry (1) factors influencing initiation of spring migration, (2) migration routes and rates in the estuary, (3) effects of environmental factors, especially water currents, on speed and direction of travel, and (4) the extent to which movement was active or passive. Detailed reports on these smolt movements in the riverine and open-water portions of the estuary are forthcoming (Fried et al. in press, LaBar et al. in press).

METHODS

Study Area

The Penobscot Estuary study area is 65 km long. The upper 40 km, from head-tide downstream, is a narrow, relatively shallow, riverine portion. The lower 25 km is a wider, deeper, open-water bay portion. The lower end of the study area is still 35 km from open sea.

Tidal currents are strong throughout, with river discharge contributing substantially to rapid ebb tide currents and net seaward flow of surface waters. Tidal height range is 3-4 m. Surface water salinities ranged from 0 ^{o}/oo at head-tide to as much as 30 ^{o}/oo at the lower end of the area.

Tracking Procedures

Standard ultrasonic tracking methods (see for example McCleave et al. 1977a, McCleave et al. 1977b) and the smallest commercially available transmitters (9 mm diameter X 33-36 mm long) were used. Transmitters were stomach emplaced. Smolt locations were usually determined every 20 min and measurements were made of water current direction, depth, temperature, salinity, wind velocity, wave direction and height, cloud cover, sun or moon visibility, and precipitation. Some additional data on water currents were obtained by tracking drift drogues for extended periods or along with 20 min smolt movements. Some smolt swimming depth information was obtained using a linear array hydrophone (Gardella and Stasko 1974).

Ultrasonic tracking was conducted early April to early June, 1975 and 1976, to follow the behavior of smolts from well before to well past the normal migration period. Most tracks were initiated by releasing a group of about 40 smolts, one of which was equipped with a transmitter; a few were begun with one to six smolts. Forty-six smolts were tracked; 34 tracks began near head-tide and 12 began 10-27 km farther downriver. Nine tracks included portions in the open water of the bay. Individual tracks lasted 1-69 h and covered 0.4-83.7 km.

RESULTS

Seasonal Timing of Migration

Smolts exhibited two distinct behavior patterns. During the premigratory phase, prior to 10 May, the 18 smolts tracked were inactive and generally remained near shore in shallow water. The few that showed some movement soon moved into shallow water and again became inactive. In contrast, nearly all of the 28 smolts released on or after 10 May quickly moved away from the release point into deeper, swift water, and made substantial seaward progress.

While 10 May was the date each year that the first long seaward movement occurred, the transition from non-migratory to migratory behavior was rapid, but not instantaneous. On 6 and 7 May two smolts made essentially no seaward progress. On 8 May each year smolts moved considerably, but with little net seaward progress. These latter two smolts may have exhibited transitional behavior.

Pre-migratory smolts had average ground speeds of 2.9 cm s^{-1} during tracks averaging 32.9 h, while migratory smolts averaged 40.1 cm s^{-1} over 22.2 h (Table 1).

River (and hatchery) water temperatures above 9° C were apparently the most important proximate factor in triggering seaward migration (Fig. 1). Greater variability in the transition to migratory behavior was observed in 1976, but is explained by the different temperature patterns in the two years. In 1975 water temperatures rose rapidly, reached 9° C on 10 May, and stayed above it thereafter. In 1976 river temperatures rose more gradually and were near 9° C from 2-10 May and again on 25 May.

Once migration began, smolt movement was no longer related to temperature. No changes in movement behavior were observed even though individual smolts in the lower part of the area encountered temperatures as low as 6° C, or as much as 10° C below the river temperature at the release point.

Smolts continued to migrate seaward throughout the study period (as late as 6 June).

Migration Routes and Rates

Five smolts were tracked continuously through the entire riverine portion of the study area. All travelled much farther (mean 58.4 km) than the shortest possible distance (34.5 km). Departures from the shortest route resulted mainly from upriver movement during flood tide. The only choice of alternate seaward routes in the riverine portion occurred at an island near the entrance to the bay. Nine of 10 smolts tracked past this choice point travelled down the shorter, deeper channel.

The route followed by smolts in the bay depended upon stage of tide when entering the bay. All made substantial direct seaward progress if they entered on an ebb tide. If smolts encountered flood tides in the upper part of the bay, they generally moved back up the bay. In the lower part of the bay smolts continued to move down the bay on both ebb and flood tides. Most of the time smolts moved in the main, deep channels, but occasionally smolts entered and milled about in shallow coves.

Smolts migrated near the surface. The mean swimming depth of one smolt for which 73 depth measurements were made over 44 h was 3 m (Fig. 2). Scattered depth observations of five other smolts gave a mean depth of 2 m (n=28). Mean ground speed (the resultant of water current movement and actual swimming) of all smolts in the migratory group (after 10 May) was about 40 cm s^{-1} (1.7 body lengths s^{-1}). Mean ground speeds were significantly greater on ebb tides than on flood tides and significantly greater in the bay than in the riverine portion.

Relation of Migration to Water Currents

Water current, from the combination of river discharge and strong tidal action, is the major transport factor in the seaward migration of smolts in the Penobscot Estuary. Furthermore, the migration of smolts seems to be largely passive drift through the estuary.

Measured 20 min smolt movement directions were usually similar to measured water current directions on both ebb and flood tide. Of the 18 smolts in the migratory group tracked in the riverine portion, ten had movement directions significantly clustered around the water current direction on both ebb and flood tides when tested with a modified Rayleigh test (Batschelet 1972). Seven more were significantly clustered on ebb tides only. In the bay all nine smolts had movement directions significantly clustered around the current direction on both ebb and flood tides.

The most convincing evidence that smolt migration through the estuary is largely passive drift was provided by comparison of the behavior of drift drogues and the behavior of smolts. Several 1, 3 and 5 m drogues were released near head-tide on ebb tides. Their speed of travel for the first 12 km (where they were picked up) (about 90 cm s^{-1}) was quite similar to the speed of smolts beginning movement on an ebb tide. Simultaneous tracking of 1 and 3 m drogues and smolts was done for five smolts for 1-5 h in the riverine portion of the estuary. Velocities of drogues closely approximated velocities of smolts, except when smolts were in shallow water or during times of tidal current reversal.

In the bay three 2 m drogues were continuously tracked for several hours -- one in the upper bay, one in mid-bay and one in the lower bay. The routes and rates of drogue travel were similar to the routes and rates of smolts in the same areas on similar stages of tide.

If the migration is essentially passive drift in surface waters, net seaward travel and ground speed should reflect the rhythmicity in tidal movement. Tides in the study area are semidiurnal. Therefore maxima and minima in net seaward travel should occur at peak ebb and peak flood tides, respectively, every 6.2 h. A maximum ground speed at peak ebb tide and a lesser maximum at peak flood tide are expected.

The expected patterns were observed in smolts in the migratory group. An approximately sinusoidal curve of net seaward travel occurred in the study area as a whole (Fig. 3A), and the pattern was similar for the riverine (Fig. 3B) and open-water portions (Fig. 3C) individually. Mean net seaward travel during peak ebb was 2.4 km h^{-1}, and there was net landward travel of 0.6 km h^{-1} at peak flood.

Two peaks of unequal magnitude in swimming speed were found in the entire study area (Fig. 4A) or the riverine and open-water portions separately (Fig. 4B,C). Mean swimming speeds ranged from 20-65 cm s^{-1} in the river and from 30-85 cm s^{-1} in open water.

Responses to Other Environmental Factors

No other environmental factor appeared to influence smolt movements, except for the importance of water temperature in initiation of migration. Similar migration behavior was noted day and night, under both clear and overcast sky, and as smolts moved into saline water.

DISCUSSION

Rising water temperature in spring seems to be the proximate trigger for smolt migration, and 10° C is often suggested as the critical temperature. When several years of data are examined from a single river, there is substantial variation in the temperature at the beginning of migration (e.g. Bakshtansky et al. 1976, Elson 1962). Österdahl (1969) cautioned that the 10° C might be coincidental rather than causative. Our data (Fried et al. in press) on the actual beginning of smolt movement as determined by telemetry from individuals fit well with the 9-10° C estimates based upon trapping records.

Calderwood (1908) stated that: "... the salmon smolts make a steady and comparatively rapid descent to the open sea, without hanging about and growing in the estuary, as sea trout appear to do, and that in making their descent they forsake the shallows for the main current." Ultrasonic tracking studies nearly 70 yr later essentially confirm these early findings, at least for hatchery-reared smolts. The journey from head-tide to open water well down Penobscot Bay, covering a distance of 45-57 km and going from water of 0 ‰ to water up to 30 ‰, usually took less than 48 h, and with few exceptions the fish moved in the main current away from the shoreline.

The simplest way to explain this seaward migration is by passive drift, and, all evidence suggests that the smolts were passively drifting. Tidal rhythmic effects on movement of smolts in estuaries obviously must be present, if the smolts are drifting on tidal currents. Smolts could speed their seaward migration by adding active behavior timed to the tidal rhythm. They could hold position on the bottom or near shore on the flood tide and drift only on ebb tides to effect a selective tidal transport as has been described for plaice (Pleuronectes platessa) (Greer Walker et al. in press). Smolts could also drift with the ebb tide and actively stem the flood tide. Some adult Atlantic salmon were reported to do the opposite to make progress up a large estuary (Stasko 1975). Smolts could also actively swim with the ebb tide. We found little or no evidence to suggest any active behavior relative to the tides in the estuary (Fried et al. in press, LaBar et al. in press).

The freshwater smolt migration is usually characterized by distinct diel rhythms, though runs in a given river may be largely nocturnal (Jessop 1975), diurnal (Solomon 1975) or seasonally changing (Österdahl 1969). This rhythmic behavior apparently is abandoned in the estuary in favor of passive drift without diel components. Such behavior in the estuary allows rapid seaward travel, while placing minimum demands on the orientational systems of the smolt in an area of deep, turbid, turbulent water.

ACKNOWLEDGMENTS

The ideas of my colleagues, Stephen M. Fried and George V. LaBar, are freely intermingled with my own in this paper. I profited from discussions of the subject with F.R. Harden Jones and G.P. Arnold. The study was funded by the U.S. Fish and Wildlife Service (contract nos. 14-16-0008-893 and 14-16-0008-2017).

REFERENCES

Bakshtansky, A.L., I.A. Barybina, and V.D. Nesterov. 1976. Changes in the intensity of downstream migration of Atlantic salmon smolts according to abiotic conditions. ICES CM 1976/M:4, 12 p.

Bartel, R. 1976. The Drava River salmon in the light of some recent tagging experiments. ICES CM 1976/M:6, 11 p.

Batschelet, E. 1972. Recent statistical methods for orientation data. In Animal orientation and navigation, p. 61-91. Ed. by S.R. Galler, K. Schmidt-Koenig, G.J. Jacobs, and R.E. Belleville. Nat. Aeron. Space Admin., Wash., D.C.

Calderwood, W.L. 1908. The Life of the Salmon, with Reference More Especially to the Fish in Scotland. Arnold, London. 160 p.

Elson, P.F. 1962. Predator-prey relationships between fish-eating birds and Atlantic salmon. Bull. Fish. Res. Board Can. 133: 1-87.

Everhart, W.H., and R.E. Cutting. 1967. The Penobscot River. Atlantic salmon restoration: Key to a model river. Atlantic Sea Run Salmon Commission. Orono, Maine. 22 p.

Fried, S.M., J.D. McCleave, and G.W. LaBar. (In press). Seaward migration of hatchery-reared Atlantic salmon (Salmo salar) smolts in the Penobscot River estuary: Riverine movements. J. Fish. Res. Board Can.

Gardella, E.S., and A.B. Stasko. 1974. A linear-array hydrophone for determining swimming depth of fish fitted with ultrasonic transmitters. Trans. Am. Fish. Soc. 103: 635-637.

Greer Walker, M., F.R. Harden Jones, and G.P. Arnold. (In press). Movements of plaice (Pleuronectes platessa L.) tracked in the open sea. J. Cons. int. Explor. Mer.

Huntsman, A.G. 1962. Method in ecology-ectology. Ecology 42: 552-556.

Jessop, B.M. 1975. Investigation of the salmon (Salmo salar) smolt migration of the Big Salmon River, New Brunswick, 1966-72. Fisheries and Marine Service, Resource Development Branch, Tech. Rep. Series MAR/T-75-1: 1-57.

LaBar, G.W., J.D. McCleave, and S.M. Fried. (In press). Seaward migration of hatchery-reared Atlantic salmon (Salmo salar) smolts in the Penobscot River estuary, Maine: Open-water movements. J. Cons. int. Explor. Mer.

McCleave, J.D., S.M. Fried, and A.K. Towt. 1977a. Daily movements of shortnose sturgeon, Acipenser brevirostrum, in a Maine estuary. Copeia 1977: 149-157.

McCleave, J.D., G.W. LaBar, and F.W. Kircheis. 1977b. Within-season homing movements of displaced mature Sunapee trout (Salvelinus alpinus) in Floods Pond, Maine. Trans. Am. Fish. Soc. 106: 156-162.

Österdahl, L. 1969. The smolt run of a small Swedish river. In Symposium on salmon and trout in streams, p. 205-215. Ed. by T.G. Northcote. Univ. of British Columbia, Vancouver.

Solomon, D.J. 1975. Observations on some factors influencing the migration of smolts of salmon (Salmo salar L.) and migratory trout (S. trutta L.) in a chalkstream. ICES CM 1975/M:11, 10 p.

Stasko, A.B. 1975. Progress of migrating Atlantic salmon (Salmo salar) along an estuary, observed by ultrasonic tracking. J. Fish. Biol. 7: 329-338.

Stasko, A.B., A.M. Sutterlin, S.A. Rommel, Jr., and P.F. Elson. 1973. Migration-orientation of Atlantic salmon (Salmo salar L.). In International Atlantic Salmon Symposium 1972, p. 119-137. Ed. by M.W. Smith,and W.M. Carter. Int. Atl. Salmon Fdn, Spec. Publ. No. 4.

Table 1. Comparison of distances and speeds of travel by pre-migratory and migratory groups of Atlantic salmon smolts in the Penobscot River estuary, Maine, USA. Tracks on 8 May 1975 and 1976 not included. Ranges given in parentheses

Smolt behavior group	Number of fish	Mean track duration (h)	Mean travel distance (km)	Mean ground speed (cm s^{-1})	Mean net seaward travel (km)
Pre-migratory 1975	10	37.3	1.5	1.1	0.8
		(19.0-69.0)	(0.4-6.2)	(0.4-7.9)	(0.0-3.7)
Pre-migratory 1976	8	27.1	5.9	6.1	4.4
		(2.6-51.7)	(0.4-19.1)	(0.3-61.5)	(0.1-11.8)
Pre-migratory, all	18	32.9	3.4	2.9	2.4
Migratory 1974, 1975	12	24.0	39.4	45.5	23.4
		(1.3-49.5)	(2.7-83.7)	(15.4-75.8)	(2.6-47.3)
Migratory 1976	16	20.9	26.6	35.5	15.5
		(1.0-47.6)	(0.6-71.8)	(4.5-90.3)	(0.2-41.8)
Migratory, all	28	22.2	32.1	40.1	18.9

FIGURE LEGENDS

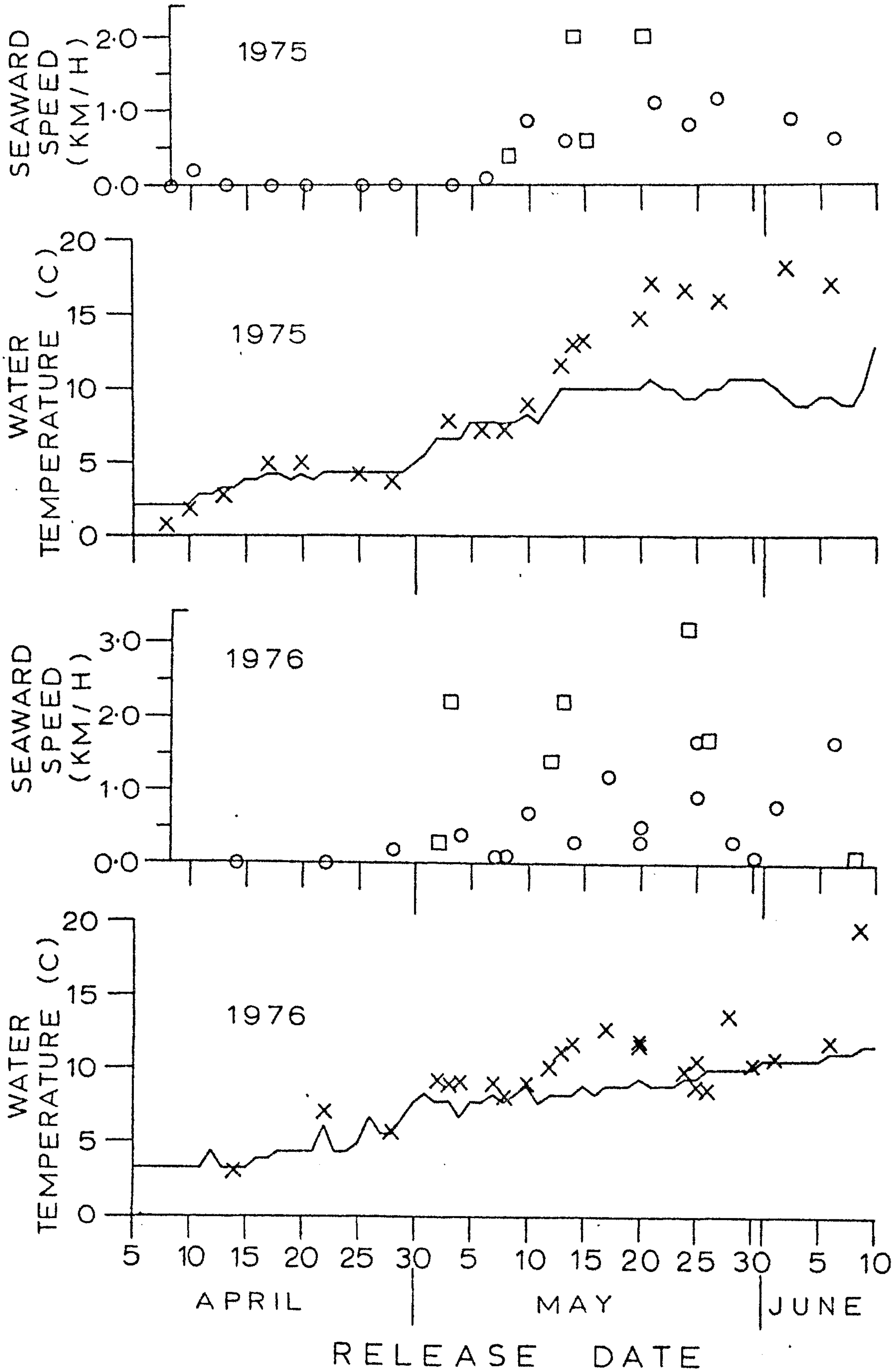
Fig. 1. Mean seaward travel rates of Atlantic salmon smolts, river water temperatures at time of release and mean daily hatchery water temperatures during ultrasonic tracking studies. Circle = smolt tracked more than 6 h, square = smolt tracked less than 6 h, X = river temperature, solid line = hatchery temperature.

Fig. 2. Swimming depth in relation to water depth, time of day and tide stage of one Atlantic salmon smolt tracked 1-3 June 1976. Each point on the upper curve represents a swimming depth measurement. Lower curve is water depth. Mean swimming depth is shown as a horizontal line.

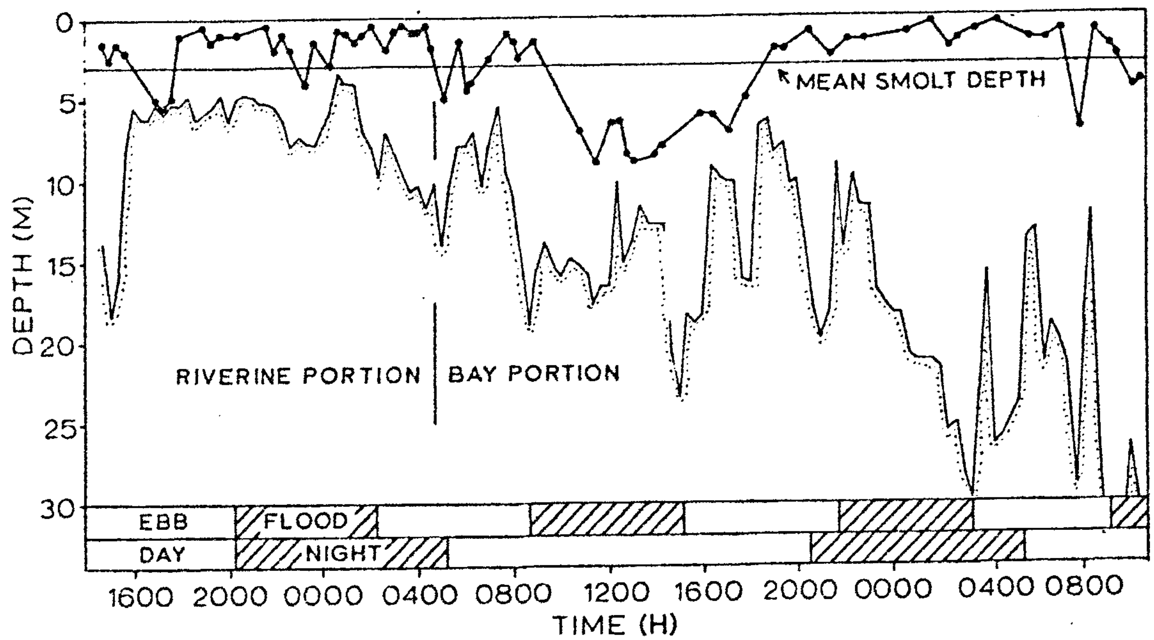
Fig. 3. Tidal pattern of mean net seaward travel of all Atlantic salmon smolts tracked on or after 10 May, 1975 and 1976. Tidal cycle plotted twice to better show pattern. Bars = ± 1 standard deviation. A. Entire study area. B. Riverine portion of estuary. C. Bay portion of estuary.

Fig. 4. Tidal pattern of mean hourly ground (swimming) speeds of all Atlantic salmon smolts tracked on or after 10 May, 1975 and 1976. Tidal cycle plotted twice. Bars = ± 1 standard deviation. A. Entire study area. B. Riverine portion of estuary. C. Bay portion of estuary.

Figure 1



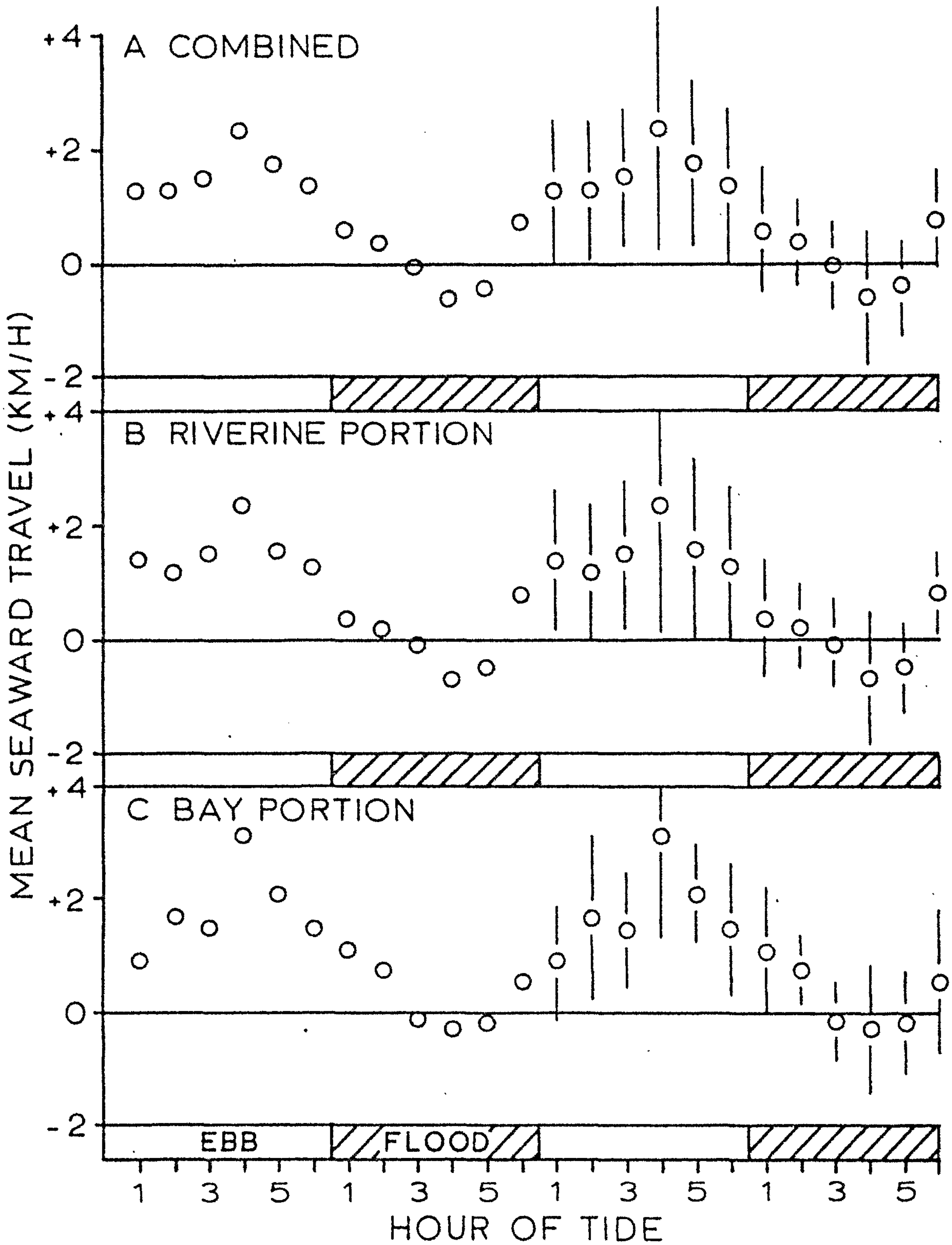
SEAWARD SPEED (KM/H)
1975
2·0
1·0
0·0
WATER TEMPERATURE (C)
1975
20
15
10
5
0
SEAWARD SPEED (KM/H)
1976
3·0
2·0
1·0
0·0
WATER TEMPERATURE (C)
1976
20
15
10
5
0
5 10 15 20 25 30 5 10 15 20 25 30 5 10
APRIL
MAY
JUNE
RELEASE DATE



DEPTH (M)
0
5
10
15
20
25
30
MEAN SMOLT DEPTH
RIVERINE PORTION
BAY PORTION
EBB
FLOOD
DAY
NIGHT
1600 2000 0000 0400 0800 1200 1600 2000 0000 0400 0800
TIME (H)

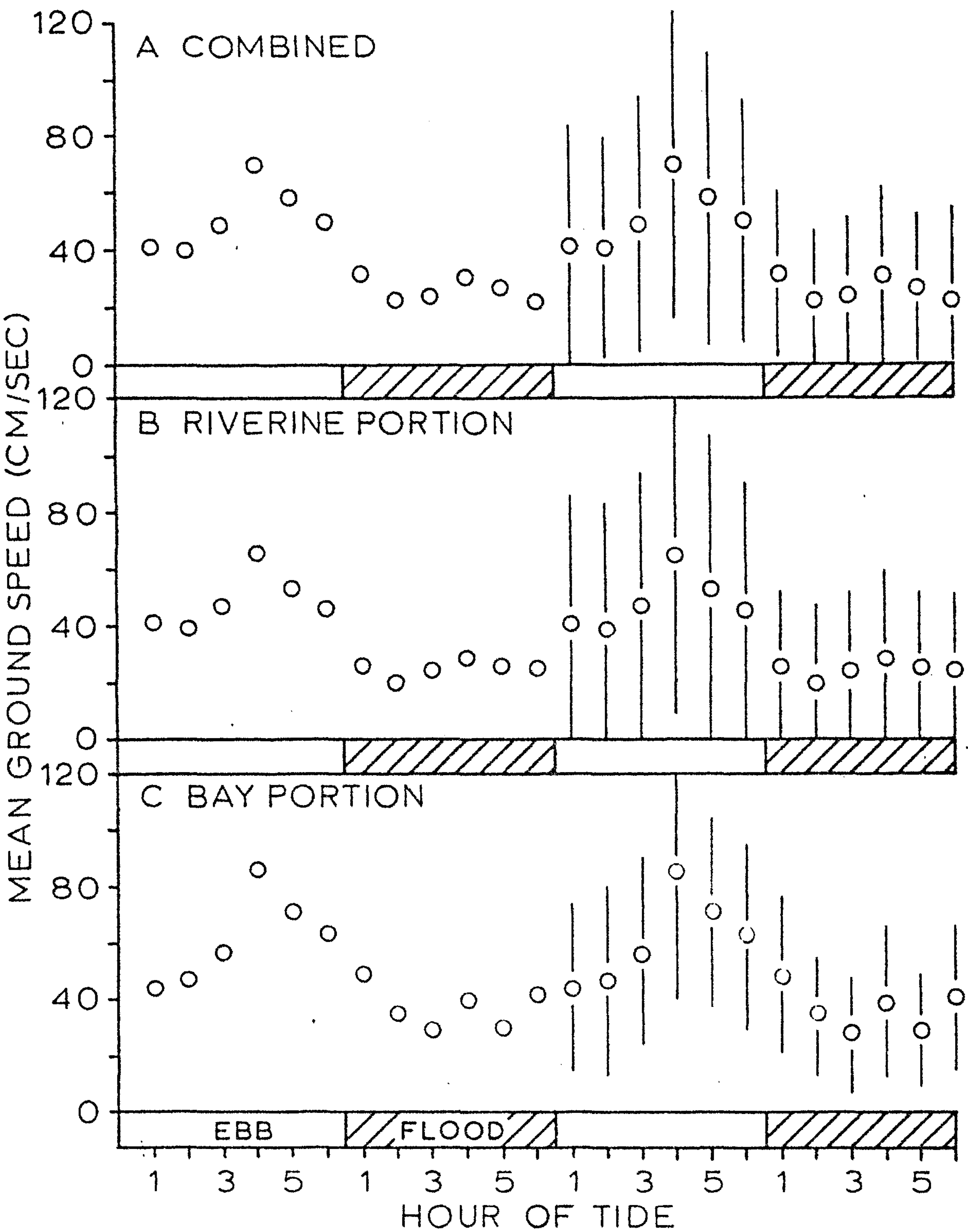
Figure 2

Figure 3



A COMBINED
B RIVERINE PORTION
C BAY PORTION
MEAN SEAWARD TRAVEL (KM/H)
+4
+2
0
-2
EBB
FLOOD
1 3 5 1 3 5 1 3 5 1 3 5
HOUR OF TIDE

Figure 4



A COMBINED
B RIVERINE PORTION
C BAY PORTION
MEAN GROUND SPEED (CM/SEC)
120
80
40
0
EBB
FLOOD
1 3 5 1 3 5 1 3 5 1 3 5
HOUR OF TIDE