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UP-ESTUARY MIGRATION OF GLASS EELS (ANGUILLA ROSTRATA) IN RELATION TO TIDAL FLOW

by

James D. McCleave and Robert C. Kleckner
Migratory Fish Research Institute
and Department of Zoology
University of Maine
Orono, Maine 04469 USA

Abstract

The depth distribution of glass eels of the American eel (*Anguilla rostrata*) on ebb and flood tides at night was determined by using vertical strings of four 0.5 m plankton nets anchored in the tidal flow of the saline, salt-wedge and freshwater portions of the Penobscot River estuary, Maine. Current velocity, temperature and salinity profiles were made periodically during the times of net sets. The glass eels utilize selective tidal stream transport to effect a migration up the estuary. In saline and salt-wedge portions of the estuary the glass eels are near the bottom on ebb tides, and move vertically into intermediate depths on flood tide apparently selecting the depth at which landward transport is fastest. There may or may not be a greater density of glass eels in the water column on the flood tide. In the freshwater, tidal portion of the estuary, the glass eels drop to the bottom on ebb tide, and move vertically throughout the water column on flood tide. Glass eel density is much greater on the flood than the ebb tide. Here landward flow lasts only a short time and is slow compared to seaward flow on the ebb tide.

INTRODUCTION

In near shore or estuarine waters the wind driven ocean currents become of far less magnitude than the tidal currents. These tidal currents offer a mechanism for shoreward migration or migration up an estuary by fishes (Harden Jones 1968) called _selective tidal stream transport_ (Greer Walker et al. 1978, Harden Jones et al. 1978). If the fish drops to the sea-bottom and holds position during the ebb tide, then moves up into the water column and drifts on the flood tide, it can be transported landward or up an estuary. Selective tidal stream transport can save up to 90% of the energy expended on migration in a tidal area by juvenile fish (Weihs 1978), and it can be used by organisms whose swimming powers are feeble compared with tidal current speeds.

It was in elvers of the European eel (_A. anguilla_) that selective tidal transport of fishes was first recognized. Usually catches of elvers were reported three to ten times greater on flood tides than on ebb tides in the Marsdiep and Texelstroom by Creutzberg (1958, 1961), though Deelder (1952) stated that at Wierbalg, farther landward in the Dutch Wadden Sea, there was no evidence elvers were selecting one tide over another for transport. Later, Deelder (1960) observed that elvers did utilize selective tidal transport in the Wadden Sea. Van Heusden (1943) is credited with the elver transport hypothesis, and he suggested the tidal selection was based upon salinity differences on the two tides (Deelder 1952, Creutzberg 1958). Later, Creutzberg (1959, 1961) showed that elvers detected the odors of natural fresh waters on ebb tides and dropped to the sea-bottom to avoid being swept outward. American elvers were also attracted to the odors, and not to the lack of salinity, in various natural waters (Miles 1968). These observations are consistent with the phenomenal olfactory powers of eels (Teichmann 1959). Deelder (1958) recognized the important point that elvers newly arrived off the Dutch coast did not prefer fresh water, but Schulz (1975), Miles (1968), and Deelder (1952) all showed that nearer shore elvers preferred fresh water.

The picture that has emerged for European elvers in the North Sea is that newly metamorphosed elvers drift with the tide, showing no freshwater preference (Deelder 1958), and are carried slowly on residual currents (Tesch 1975). When the elvers are physiologically ready and fresh water can be detected (Schulz 1975, Miles 1968), the elvers switch from drift to selective tidal transport (Creutzberg 1958, 1961). At the upper limit of tidal influence they may use a combination of tidal transport and active swimming (Tesch 1965). Finally, they exhibit positive rheotaxis and swim upstream (Deelder 1958).

The question of selective tidal transport of glass eels has never been carefully examined (1) in relation to tidal current flow and salinity stratification in an estuary, and (2) from the standpoint of estuarine migration rate. Further, the phenomenon has not been documented for glass eels of _A. rostrata_. The purpose of our continuing study is to do so, and preliminary results are reported here.

METHODS

Study Area. The Penobscot Estuary study area is 47 km long. The upper 41 km, from head-tide downstream, is a narrow, relatively shallow, riverine portion. The lower

6 km is a wider, deeper, open-water portion. The study area is separated from the open sea by 50 km long Penobscot Bay. Tidal currents are strong (up to 1.1 m s^{-1}), and river discharge contributes substantially to rapid ebb tide currents and net seaward flow of surface waters. Tidal height range is 3-5 m. Salinities ranged from 0 ^{o}/oo at the upper end to 34 ^{o}/oo at the lower end of the study area.

Three sampling locations were chosen near mid-channel to represent saline, salt-wedge and tidal freshwater portions of the estuary. The seaward station, 16 - 20 m deep, was saline, generally above 30 ^{o}/oo except in the upper 6 m where salinities down to 16 ^{o}/oo were observed. The intermediate station, 9 - 13 m deep, was usually highly stratified, with penetration of saline water (16 - 26 ^{o}/oo) below nearly fresh surface water and with a steep vertical salinity gradient. The landward station, 9 - 14 m deep, was unstratified and nearly fresh water (<1 ^{o}/oo). On the final sampling date the intermediate station was also unstratified and had nearly fresh water (<2 ^{o}/oo).

Sampling Gear. Vertical distribution and density of elvers was sampled with buoyed and anchored plankton nets (modified from Graham and Venno 1968) which utilize the "towing power" of the tidal flow. Each set consisted of four 0.5 m diameter, 2.0 m long plankton nets of 0.75 mm mesh attached to a line anchored to the bottom and buoyed at the surface. A vane above each net oriented the net into the current. A calibrated flow meter was placed in the mouth of each net. A detachable cod end bucket served as an initial preserving container for each plankton sample.

Sampling Plan. Sampling was done at night to eliminate phototaxis as a complicating or masking feature to tidal influence on elver behavior. Nights were chosen when a slack tide (high or low) occurred near the middle of the night. Nets were set at dusk about one half hour after sunset, and were fished on one tide until near slack water, when the nets were retrieved. The cod end buckets were changed and the nets were reset to fish the other tide until near dawn.

Each station was fished three times at approximately biweekly intervals during the period 25 March - 2 May 1980. Three replicate sets of nets were fished at each station on each sampling night. Usually seven or eight vertical profiles of current velocity, salinity and temperature were measured near the station being fished on a given night.

Analysis. Elvers were sorted from the catches and enumerated with respect to station, tide, depth of net and replication. Volume of water strained by each net was calculated from flow meter readings, and elver catches were expressed as number of elvers per 100 m^3 of water.

Each complete sampling of one station was considered a three-way factorial experiment, with tide, depth and replication as the factors. G (or log liklihood ratio) tests (Sokal and Rohlf 1969), nonparametric analogs of analysis of variance, were used to examine main effects and interactions. Tide, depth, and tide-depth interaction effects are the crucial features in interpreting selective tidal transport schemes.

Estimates of the average distance traveled by an elver over the period of ebb and flood net sets were calculated for selected stations and dates. We assumed the catch rate of each of the four nets was representative of that portion of the water column, and that the current speed at the depth of each net was representative of that portion of the water column. Thus the water column was viewed as four filaments of water traveling at a certain speed with a certain elver density. Average speeds were determined from current profiles and times between profiles. Average distance was calculated from the proportion of elvers moving at different speeds at the four depths. On the tide with the greater catch rate 100% of the elvers were assumed to be in the water column; on the other tide proportionally fewer were assumed to be in the water column, depending on relative ebb and flood catch rates.

RESULTS

Tidal Transport Behavior. Elvers (glass eels) of the American eel definitely utilize selective tidal stream transport to effect a migration up the Penobscot Estuary, however, their mechanism of utilizing the tides differs in stratified and unstratified portions of the estuary.

In the stratified portion elvers tend to be found low in the water column, largely at net depth 4, on ebb tides, and slightly higher in the water column, largely at net depth 3, on flood tides (Table 1). Usually this effect of net depth is statistically significant, especially when ebb and flood tides are considered separately (Table 3). Overall catch rates on flood tide may or may not be significantly greater than on ebb tide (Tables 1, 3). Thus elvers move lower in the water column on ebb tide, and some may also leave the water column completely on ebb tide.

At the seaward and intermediate stations (when stratified) water moves up the estuary fastest and for the longest time on flood tides at the depths of nets 3 and 4 (Fig. 1). Conversely water flows seaward rapidly and for a long period at the depths of nets 1 and 2. The behavior observed insures that the elvers are transported landward rapidly on the flood tide and are not swept back to sea on the ebb tide. They may even experience landward transport deep in the water column through most of the ebb tide at the intermediate station.

In the unstratified portion of the estuary elvers tend to be spread throughout the water column on flood tide, and drop out of the water column on ebb tide (Table 2), so that catch rates on flood tides are significantly greater than on ebbs (Table 3). The effect of net depth is insignificant on flood tides, and usually so on ebb tides (Table 3).

In the absence of salinity stratification both seaward and landward flows are more uniform from top to bottom (Fig. 2). Furthermore, ebb currents greatly exceed flood currents all the way to the bottom. Again the observed behavior is appropriate to effect landward transport and prevent seaward transport. Here the elvers must leave the water column entirely to avoid seaward transport on ebb tides.

The change in behavior from stratified to unstratified portions of the estuary is apparently due to changes in hydrography rather than location in the estuary. Supporting evidence is provided by the catches at the intermediate station on 9-10 April and 1-2 May (Table 2). On the former night the station was stratified (Fig. 1), and elvers were caught in the pattern typical for a stratified portion (Tables 1, 3), while on the latter night, due to increased run-off, the station was unstratified with little salinity and elvers were caught in the pattern typical for an unstratified portion (Tables 2, 3).

Tidal Transport Distance. The distance an average elver moves on a given tidal cycle is variable depending upon the combination of behavior and tidal velocities at various depths. The latter depend upon tidal height range and freshwater discharge at a given station. Selected specific examples can be given, however.

At the intermediate (stratified) station on 9-10 April an average elver would have moved 655 m seaward on the ebb and 4220 m landward on the flood during the time of net set. Thus a net landward transport of 3565 m could have occurred over the net set.

At the landward (unstratified) station on 15-16 April an average elver would have moved 2165 m up-estuary on the flood, 1220 down-estuary on the ebb, for a net potential up-estuary transport of 945 m during the net set. At the intermediate station, when unstratified on 1-2 May an elver might have accomplished a 1930 m up-estuary transport.

These calculations did not always show net landward movement. For example, at the landward station on 30 April-1 May even though elver density was much lower and the elvers were much lower in the water column on ebb tide, the ebb flow was so strong and persisted so long that an average net seaward transport of 2025 m was calculated for the net set. The only other calculated occurrences of net seaward travel were at the seaward station, where sample sizes were so low on all three dates as to render transport calculations meaningless.

DISCUSSION

The new information provided by this study is (1) a confirmation that elvers of Anguilla rostrata do indeed utilize selective tidal stream transport during their migration up estuaries, as previously reported for elvers of A. anguilla (Creutzberg 1958, 1961), and (2) that the behavior associated with selective tidal transport is modified to fit existing hydrographic conditions. In a well stratified estuary the fastest landward transport would occur if elvers left the water column or were quite near the bottom on ebb tide and moved up, but remained below the halocline, on flood tide. This apparently occurred at the intermediate station. In tidal freshwater areas fastest landward transport would occur if elvers dropped completely out of the water on ebb tide and distributed themselves anywhere in the water column on flood tide. This also occurred at our unstratified stations.

The calculations of transport distances presented here should be considered only as approximations of the potential for transport. They are based on a number of simplifying assumptions and only on nighttime catches. None-the-less they are calculated from actual hydrographic data obtained simultaneously with the elver samples. We do know that transport is not a continuous process since, for example, on 25-26 March selective tidal transport occurred at the intermediate station, but only one elver was caught at the landward station one week later. The stations are only about 8 km apart, a distance easily covered in just two or three tides. A concentration of elvers was reported in an area of 1-2 $^{o}/oo$ salinity in the Elbe Estuary by Tesch (1971), who felt there was a delay in the migration just below full fresh water.

These preliminary studies have only considered night movements in mid-channel. In 1981 we will compare catches between day and night and between mid-channel and near shore. With these additional data better estimates can be made of transport distances and numbers of elvers transported past a given point.

ACKNOWLEDGMENTS

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Table 1. Catch rates of elvers at different depths on ebb and flood tides in stratified portions of Penobscot Estuary, Maine, on selected sampling dates.

Net number	Depth range of net through tidal cycle, m	Depth of net as percentage of water depth	Catches of elvers per 100 m^3 water (Numbers of elvers in parentheses) Ebb tide	Flood tide	Mean
			Intermediate Station, 25-26 March		
1	1.1 - 1.6	13	0.12 (7)	0.28 (1)	0.20 (8)
2	3.8 - 5.5	42	0.62 (13)	0.00 (0)	0.31 (13)
3	6.0 - 8.7	67	0.62 (6)	5.82 (55)	3.22 (61)
4	7.3 - 11.3	81-87	1.02 (3)	2.45 (2)	1.74 (5)
Mean	-	-	0.60 (29)	2.14 (58)	1.37 (87)
			Intermediate Station, 9-10 April		
1	1.1 - 1.6	13	0.07 (3)	0.10 (1)	0.08 (4)
2	3.8 - 5.5	42	0.10 (2)	0.18 (3)	0.14 (5)
3	6.0 - 8.7	67	0.14 (1)	2.08 (61)	1.11 (62)
4	7.3 - 11.3	81-87	1.84 (5)	0.00 (0)	0.92 (5)
Mean	-	-	0.54 (11)	0.59 (65)	0.56 (76)
			Seaward Station, 16-17 April		
1	1.2 - 1.5	8	0.00 (0)	0.04 (1)	0.02 (1)
2	5.7 - 7.6	38	0.03 (1)	0.19 (4)	0.11 (5)
3	10.0 - 13.3	66	0.20 (3)	0.24 (5)	0.22 (8)
4	13.3 - 18.3	88-91	1.29 (5)	0.00 (0)	0.64 (5)
Mean	-	-	0.38 (9)	0.12 (10)	0.25 (19)

Table 2. Catch rates of elvers at different depths on ebb and flood tides in fresh-water tidal (unstratified) portions of Penobscot Estuary, Maine, on selected sampling dates.

Net number	Depth range of net through tidal cycle, m	Depth of net as percentage of water depth	Catches of elvers per 100 m^3 water (Numbers of elvers in parentheses)		
			Ebb tide	Flood tide	Mean
Landward Station, 15-16 April					
1	1.0 - 1.8	13	0.00 (0)	1.40 (11)	0.70 (11)
2	3.4 - 5.9	42	0.00 (0)	0.65 (4)	0.33 (4)
3	5.4 - 9.4	67	0.00 (0)	0.70 (4)	0.35 (4)
4	6.3 - 12.3	78-88	0.24 (2)	0.00 (0)	0.12 (2)
Mean	-	-	0.06 (2)	0.69 (19)	0.37 (21)
Landward Station, 30 April- 1 May					
1	1.1 - 1.5	13	0.00 (0)	4.05 (30)	2.03 (30)
2	3.8 - 5.1	42	0.13 (2)	1.37 (9)	0.75 (11)
3	6.0 - 8.1	67	0.19 (3)	2.74 (15)	1.46 (18)
4	7.3 - 10.3	81-85	3.00 (12)	4.26 (14)	3.63 (26)
Mean	-	-	0.83 (17)	3.10 (68)	1.97 (85)
Intermediate Station, 1-2 May					
1	1.1 - 1.6	13	0.12 (1)	1.74 (14)	0.93 (15)
2	3.8 - 5.5	42	0.00 (0)	0.80 (3)	0.40 (3)
3	6.0 - 8.7	67	0.00 (0)	1.64 (6)	0.82 (6)
4	7.3 - 11.3	81-87	0.00 (0)	0.51 (1)	0.25 (1)
Mean	-	-	0.03 (1)	1.17 (24)	0.60 (25)

Table 3. Summary of non-parametric, G-statistic analysis of elver catch rates presented in Tables 1 and 2. Depth ranks are net numbers ranked in order of descending catch rate. (Net 1 = shallowest. Tide X Depth = tide-depth interaction. F = catch rate greater on flood tide than on ebb tide).

		Ebb tide alone		Flood tide alone	
Hypothesis	Significance probability, p	Depth rank	Significance probability, p	Depth rank	Significance probability, p
Intermediate Station, 25-26 March					
Tide (F)	<0.001				
Depth	<0.001	4 2 3 1	>0.05	3 4 1 2	<0.001
Tide X Depth	<0.05				
Intermediate Station, 9-10 April					
Tide (F)	>0.05				
Depth	<0.05	4 3 2 1	<0.05	3 2 1 4	<0.001
Tide X Depth	<0.001				
Seaward Station, 16-17 April					
Tide	>0.05				
Depth	>0.05	4 3 2 1	<0.05	3 2 1 4	>0.05
Tide X Depth	>0.05				
Landward Station, 15-16 April					
Tide (F)	<0.01				
Depth	>0.05	4(3 2 1) (tied)	>0.05	1 3 2 4	>0.05
Tide X Depth	>0.05				
Landward Station, 30 April-1 May					
Tide (F)	<0.001				
Depth	<0.001	4 3 2 1	<0.001	4 1 3 2	>0.05
Tide X Depth	<0.01				
Intermediate Station, 1-2 May					
Tide (F)	<0.001				
Depth	>0.05	1(2 3 4) (tied)	>0.05	1 3 2 4	>0.05
Tide X Depth	>0.05				

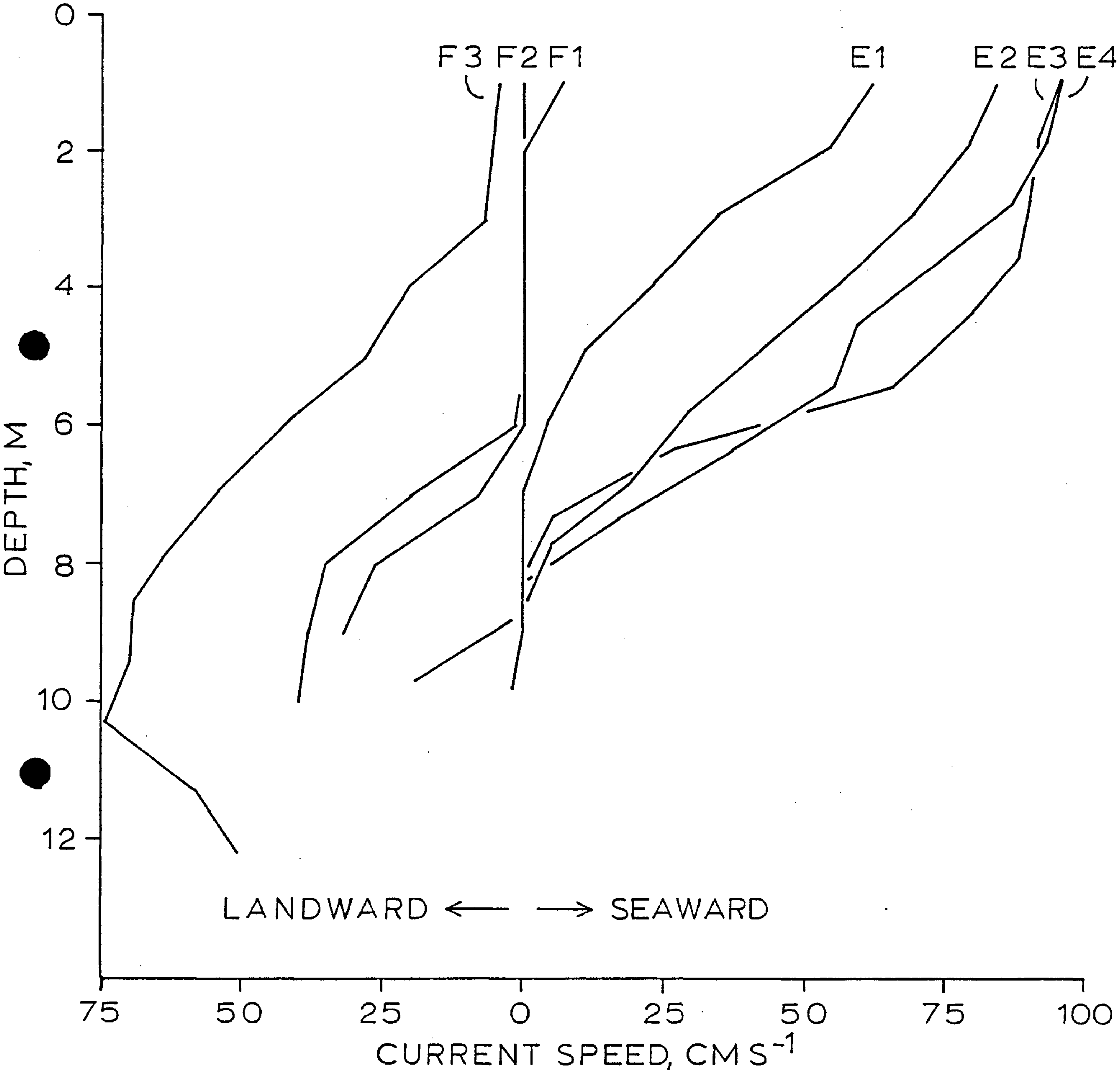

Figure 1. Water current speed profiles made during elver sampling at the intermediate station on 9-10 April 1980. Ebb tide profiles E1-E4 were at the time of high tide plus 1.4 hr, 2.6 hr, 3.5 hr, and 4.7 hr, respectively. Flood tide profiles F1-F3 were at the time of low tide plus 1.0 hr, 2.0 hr and 3.1 hr, respectively.

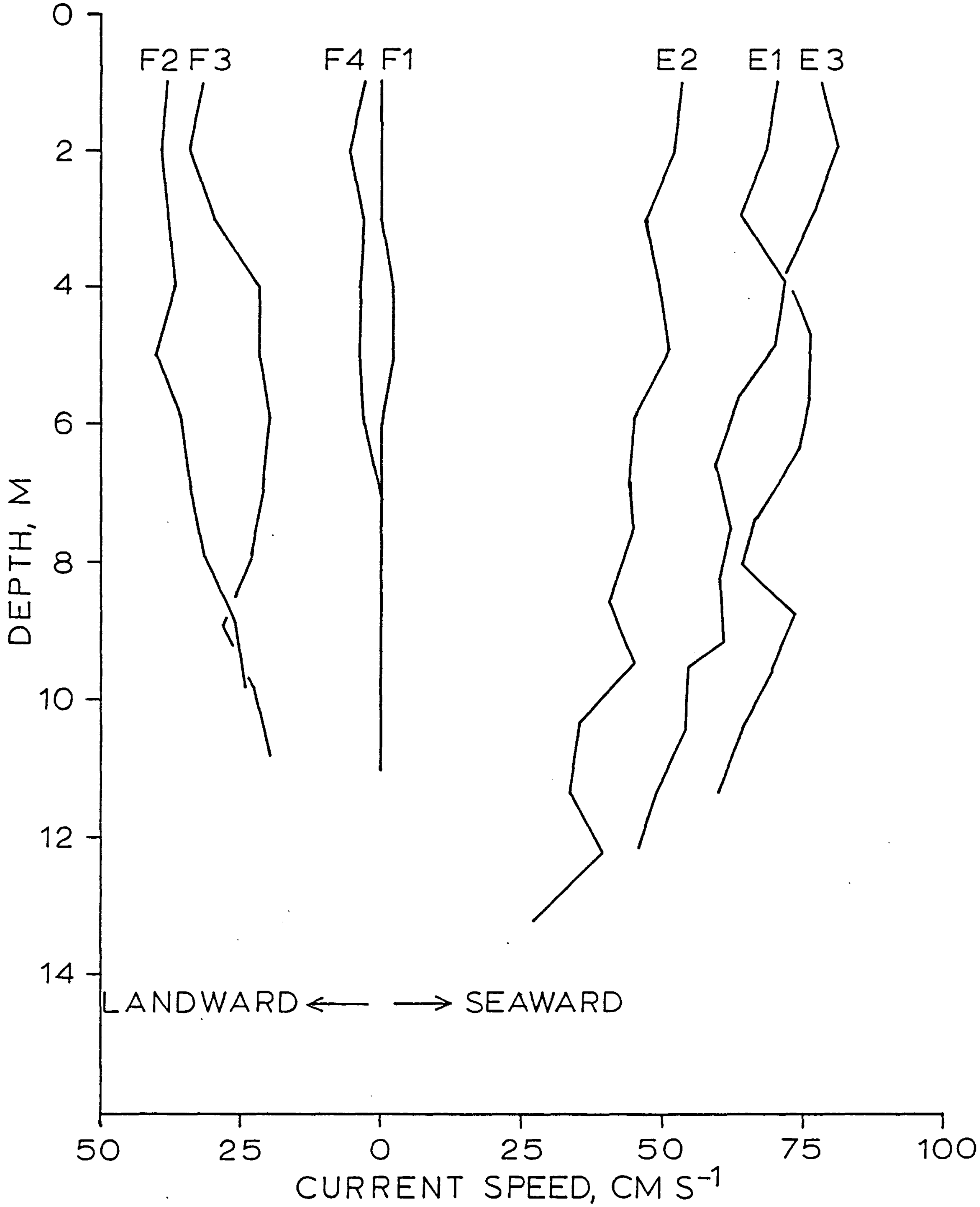

Figure 2. Water current speed profiles made during elver sampling at the landward station on 15-16 April 1980. Flood tide profiles F1-F4 were at the time of low tide plus 2.5 hr, 3.5 hr, 4.4 hr, and 4.9 hr, respectively. Ebb tide profiles E1-E3 were at the time of high tide plus 0.6 hr, 1.7 hr and 2.5 hr, respectively.