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THE MOVEMENTS OF ATLANTIC SALMON (*Salmo salar* L.) IN THE ESTUARY OF THE ABERDEENSHIRE DEE IN RELATION TO ENVIRONMENTAL FACTORS: III. CIRCADIAN AND CIRCATIDAL PATTERNS OF MOVEMENT

G W Smith and I P Smith

SOAFD Marine Laboratory
PO Box 101, Victoria Road
Aberdeen, AB9 8DB
Scotland, UK

(ei Salmo salar ee)

SUMMARY

Hourly fish counts recorded at a resistivity counter sited in the lower reaches of the River Dee, 1.5 km upstream from the limit of normal tidal influence, have been analysed. Upstream movements over the counter showed that salmon moved largely at night. There was no indication from the counter data, however, that tidal phase had any significant effect on the frequency of salmon movement into the river.

The movements of returning adult salmon fitted with transmitting tags were recorded past a sonar buoy deployed in the estuary and an Automatic Listening Station (ALS) deployed in the river, 750 m below the fish counter position. During migration upstream through the estuary and into the river, salmon movement through the estuary was significantly associated with tidal phase (Rayleigh test; N=10, z=3.69, P<0.025), having a mean value some 40 minutes before low water. There was no statistically significant association between tidal phase and salmon movement past the ALS in the river, however (Rayleigh test; N=10, z=2.85, P>0.1).

It is suggested that variations in swimming speed between different salmon may explain differences in the relationship between fish migration and tidal phase found in the estuary and during river entry. It is further suggested that interpretation of migratory behaviour from observations at arbitrary points along a salmon's migration route should be treated with caution and that comparisons of the environmental factors associated with the *initiation* of upstream migration through the estuary and into the river may provide more biologically meaningful results and greater consistency of findings between river systems.

INTRODUCTION

Although river flow is generally accepted as the dominant factor controlling upstream migration in Atlantic salmon (*Salmo salar* L.) (Huntsman, 1948; Hayes, 1953; Banks, 1969; Clarke *et al.,* 1991; Smith *et al.,* 1994) other environmental factors such as light level, temperature, tide and wind may also affect river entry (Banks, 1969). The relationship between time of day and salmon movement has been well documented. Hayes (1953), for example, found that fish generally moved into freshwater at dusk, while Potter (1988) noted that fish generally entered the River Fowey at night except during periods of increased river flow.

The relationship between tidal phase and the upstream migration of salmon into rivers is less clear. Salmon often move upstrean along estuaries on flood tides (Stasko, 1975; Brawn, 1982; Potter, 1988; Priede *et al.,* 1988). Published studies, however, report much greater variability between rivers with respect to the relationship between tidal phase and river entry, (Hayes, 1953; Priede *et al.,* 1988). Indeed, salmon enter some rivers at all stages of the tidal cycle (Potter, 1988; Webb, 1989; Potter *et al.,* 1992).

The aim of the present study was to investigate the extent to which salmon displayed circadian and circatidal patterns in their movements into the Aberdeenshire Dee, using both the records from an automatic fish counter located upstream of the tidal limit and from data derived from tracking returning adult salmon tagged with transmitting tags in the lower River Dee estuary.

MATERIAL AND METHODS

Analysis of Fish Counter Records

An automatic resistivity counter (Dunkley and Shearer, 1982; Holden, 1988) is located on a Crump weir (Dunkley and Shelton, 1991) approximately 1.5 km upstream from the limit of normal tidal influence. Hourly counts of the upstream movements of fish past the counter have been examined from a period encompassing one monthly cycle of spring and neap tides. A period was chosen (11 June to 13 July 1994) with relatively constant, moderately low river flow. The mean daily river flow during this period was 17.85 m s^{-1}, a discharge rate exceeded on 77% of days over the previous 20 years. Hourly tidal levels in the estuary were estimated with a tidal prediction program ("Tidecalc"; Anon., 1992).

There have been recent indications that the accuracy of the counter deteriorates at higher water levels (D A Dunkley, *pers. comm.*). This was not considered to be a problem during the present study period due to the relatively low river flows. There is no reason to suspect that the accuracy of the counter varied either with state of tide or time of day. Thus fluctuations in the counts at the counter in relation to either of these factors should reflect changes in the numbers of salmon moving over the counter.

Tracking Salmon Tagged with Transmitters

Returning adult salmon for radio tagging were intercepted by fixed engine (Shearer, 1992) at the mouth of the estuary. The fish were anaesthetized, a transmitting tag pushed gently into the stomach via a perspex tube placed in the mouth, and the fish was allowed to recover for up to 10 minutes before being returned to the water close to the point of capture (Hawkins and Smith, 1986; Smith *et al.*, 1995).

The transmitting tags used in the study were developed by MAFF, Lowestoft and were combined Acoustic Radio Tags (CARTs) (Solomon and Potter, 1988) which transmitted both an ultrasonic signal, allowing the fish to be tracked in saline conditions in the estuary, and a radio signal which was used to detect the salmon's subsequent entry into fresh water. The ultrasonic signal was detected by a sonar buoy (Solomon and Potter, 1988; Potter *et al.*, 1992) in the estuary, some 3 km from the mouth. In total, over 90% of the activity of tagged salmon in the estuary took place downstream of the sonar buoy (Smith *et al.*, 1995). The movements of tagged salmon into the river were detected by an Automatic Listening Station (ALS) (Hawkins and Smith, 1986) deployed above the head of tide, 750 m downstream of the fish counter position.

RESULTS

Analysis of Fish Counter Records

Upstream movements were predominantly nocturnal throughout the period analysed; 80.2% of upstream counts were registered between the hours of sunrise and sunset even though these constituted only 25.9% of the time (Goodness of fit test that the number of nocturnal movements was proportional to the length of the night: χ^2=3582, P<0.001).

Tides did not appear to influence the timing of upstream movements by salmon over the counter (Fig. 1). The greatest counts in each 24 hour period occurred consistently between 2200 and 0100 hrs GMT, regardless of when high or low tide occurred. There was no indication that the number of nocturnal or diurnal upstream movements over the counter was affected either by tidal height (Fig. 2) or tidal phase (Fig. 3). Upstream counts were slightly greater, on average, during low compared with high tidal levels and during ebbing compared with flooding tides, but these differences were not statistically significant (three way analysis of variance, with the factors of day (day/night), tidal height (low: 0.34-1.66, mid: 1.66-2.98, high: 2.98-4.30 m above chart datum) and tidal phase (ebb/flood): tidal height, $F_{2,782}$ = 0.62, P = 0.539; tidal phase, $F_{1,782}$ = 1.73, P = 0.189; time of day, $F_{1,782}$ = 871.47, P = <0.001). Analysis of tidal phase as a phase angle ranging from 0° at high tide to 180° at low tide and 360° at the next high tide in 30° categories also revealed no significant tidal influence on salmon movements over the counter ($F_{11,768}$ = 1.109, P = 0.351).

Tracking Salmon Tagged with Transmitters

During the tracking study, salmon entered the river up to 38 days after being tagged in the estuary (Smith and Hawkins, 1995). The final migration upstream through the estuary and into the river was recorded for 10 of these fish. The time taken for individual fish to move between the sonar buoy in the estuary and ALS above the head of tide varied between 80 minutes and 8 hours resulting in rates of progress for individual fish which ranged from 0.1 m s^{-1} to 0.65 m s^{1} (Smith *et al.*, 1995).

The phase of the tide associated with fish movements was calculated from published tide tables. During migration up through the estuary and into the river, salmon movement past the sonar buoy in the estuary was significantly associated with tidal phase (Rayleigh test; N=10, z=3.69, P<0.025), having a mean value some 40 minutes before low water (Fig. 4a). There was no statistically significant association between tidal phase and salmon movement past the ALS in the river, however (Rayleigh test; N=10, z=2.85, P>0.1) (Fig. 4b). Thus tagged fish whose migration past a given point in the estuary showed a statistically significant relationship with tidal phase, showed no such relationship when recorded passing a point in the river some 3 km upstream.

A simple analysis illustrates how, given a range of individual rates of progress, the association between the movements of a group of fish and tidal phase varies according to where along the migration route the observations are recorded. If it is assumed that 10 fish start from the same point at the same time and move at the speeds observed in tagged salmon in the present study (Smith *et al.*, 1995), it is possible to calculate the degree of association between that group of fish and the tidal cycle at a series of points at successively greater distances from the starting point. Estimates of r (the mean resultant, a measure of how closely the data are concentrated together, Fisher, 1993) generally declined with distance (Fig. 5a). At distances greater than 6.5 km from the starting point, the simulation indicates that no statistically significant relationship with tide can be demonstrated. The particular phase of the tide with which recorded movement appeared to be associated was also sensitive to the distance from the starting point taken to record the passage of fish (Fig. 5b).

DISCUSSION

As with a number of previous studies (Hayes, 1953; Potter, 1988; Dunkley and Shearer, 1982), analysis of fish counts showed that salmon movement into the Aberdeenshire Dee was predominantly nocturnal. The relationship between the upstream movements of salmon and the tidal cycle appeared more complex, however. Analysis of the tracking data suggests that, when migrating into the river, salmon tend to move through the estuary around low water. Analysis of both tracking and counter data, however, suggest no relationship between tidal phase and movement into the river.

The fish counter is located 1.5 km upstream from the limit of normal tidal influence. Tracking studies undertaken in the area before the counter was constructed showed that salmon, under a wide range of flow conditions, generally moved rapidly through the area (Hawkins and Smith, 1986; Smith *et al.*, 1986; Hawkins *et al.*, 1990). Tracking studies currently being undertaken in the lower Dee similarly indicate rapid movements of salmon through the lower reaches of the Dee and over the fish counter.

There is no consensus in the literature as to the relationship between tidal phase and river entry. Jackson and Howie (1967) found that river entry was generally associated with the ebb tide, while a number of authors have found no particular relationship between river entry and tidal phase (Potter, 1988; Webb, 1989; Potter *et al.*, 1992). Given the wide variation in physical, chemical and hydrographic features between estuaries, it is perhaps not surprising to find little consistent pattern in the movement of fish in one estuary when compared with another.

However, analysis presented in the present study suggests that, given variation in the rates of progress between individual salmon, both the degree of association with the tidal cycle (Fig. 5a) and also the phase of the cycle associated with movement (Fig. 5b) may be very sensitive to where the fish are monitored in relation to where they initiated their upstream migration into the river. Individual salmon may also initiate migration into the river from a range of holding areas within an estuary (Smith *et al.*, 1995). This behaviour further decreases the likelihood of demonstrating a statistically significant relationship between tidal phase and fish movement at some distance upstream, particularly in estuaries which are relatively long and which have suitable holding areas for salmon which are widely dispersed.

Similarly, movement past the sonar buoy in the estuary must also have been initiated at some distance downstream and at some point earlier in the tidal cycle than that detected by the buoy. Thus, although recorded movements in the estuary were, on average, associated with a point some 40 minutes below low water, the initiation of the salmons' migration into the river may actually tend to occur somewhat earlier in the tidal cycle.

One explanation for why rivers vary with respect to the relationship between tidal phase and river entry is that river entry may be a relatively arbitrary point at which to monitor the return migration of the salmon. Such analyses may be sufficient to investigate the relationship between salmon movement and the major factors which affect it, such as river flow and time of day. However, to investigate the role of environmental factors which perhaps exert a weaker effect on salmon movement, it may be biologically more meaningful to study the environmental conditions in which fish indicate their movement up through the estuary and into the river. Although such investigations may be intrinsically more difficult to carry out, they may lead to a greater consistency between studies on different river systems. The present study suggests that migration may be initiated during the ebb tide in the River Dee although the biological significance of that phase of the tide to the returning adult salmon remains to be determined.

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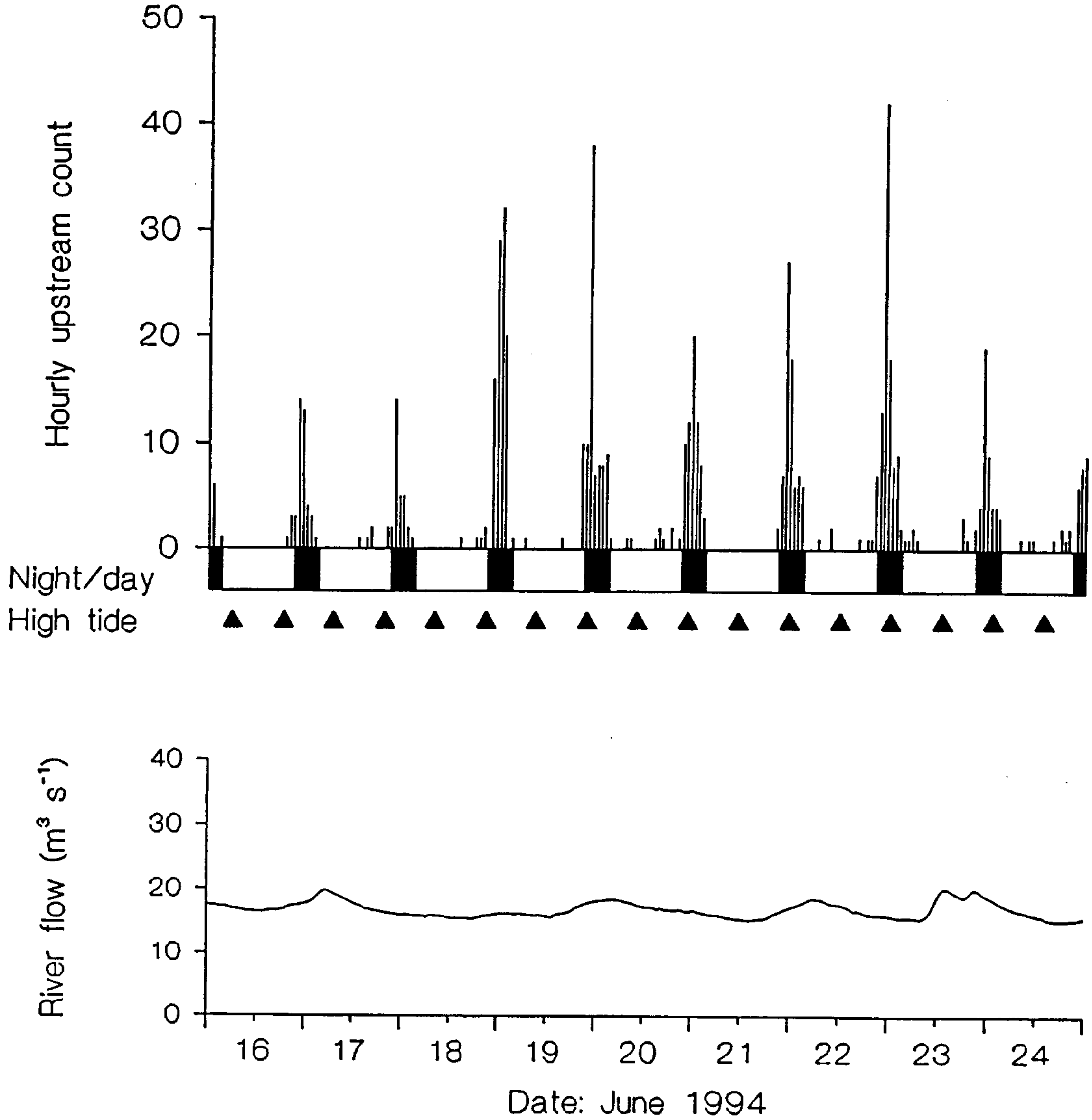

Figure 1 Hourly upstream counts over the fish counter in relation to time of day, high tide and river flow. The time of high tide is indicated by the apex of the symbol "▲". Night is indicated by the black boxes and day by the white boxes.

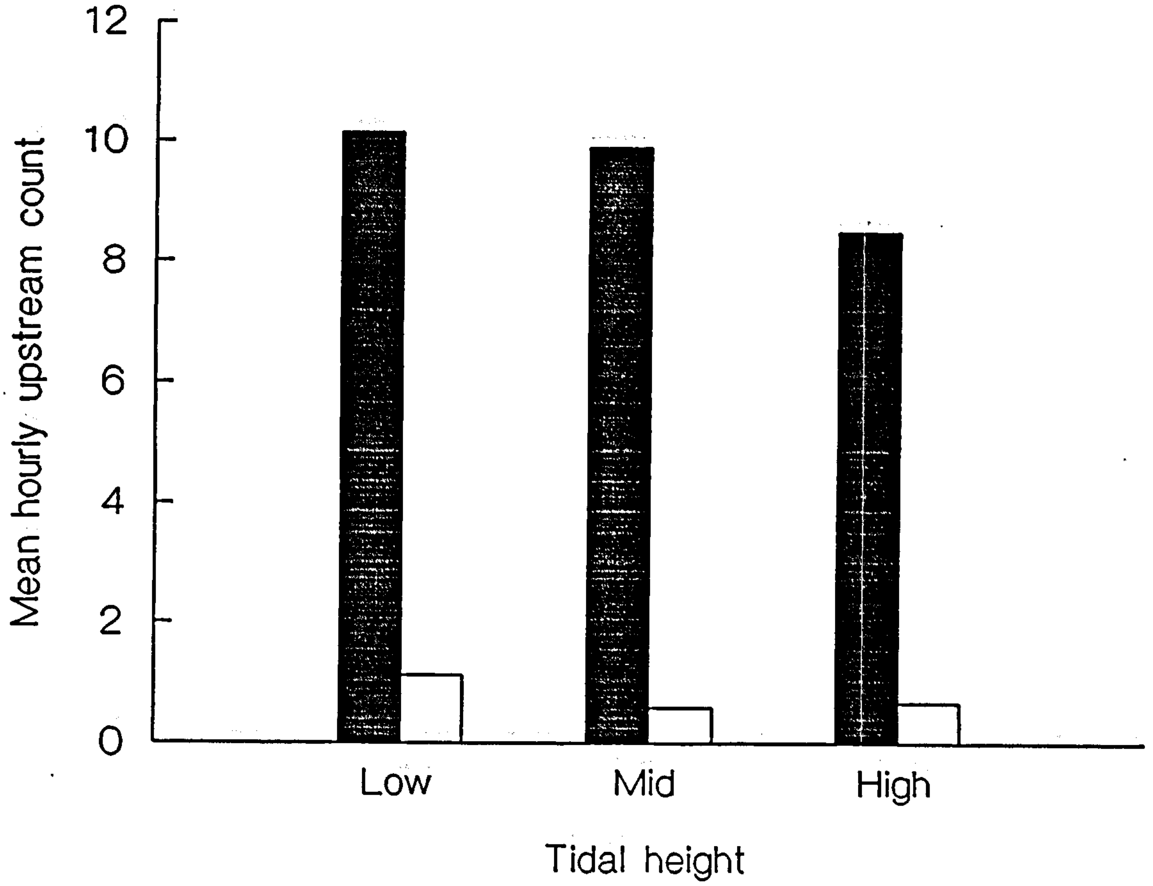

Figure 2 . Mean hourly upstream count over the fish counter during the night (black boxes) and day (white boxes), in relation to tidal height in Aberdeen harbour (Low: 0.34 to 1.66; Mid 1.66 to 2.98; High: 2.98 to 4.30 m above chart datum).

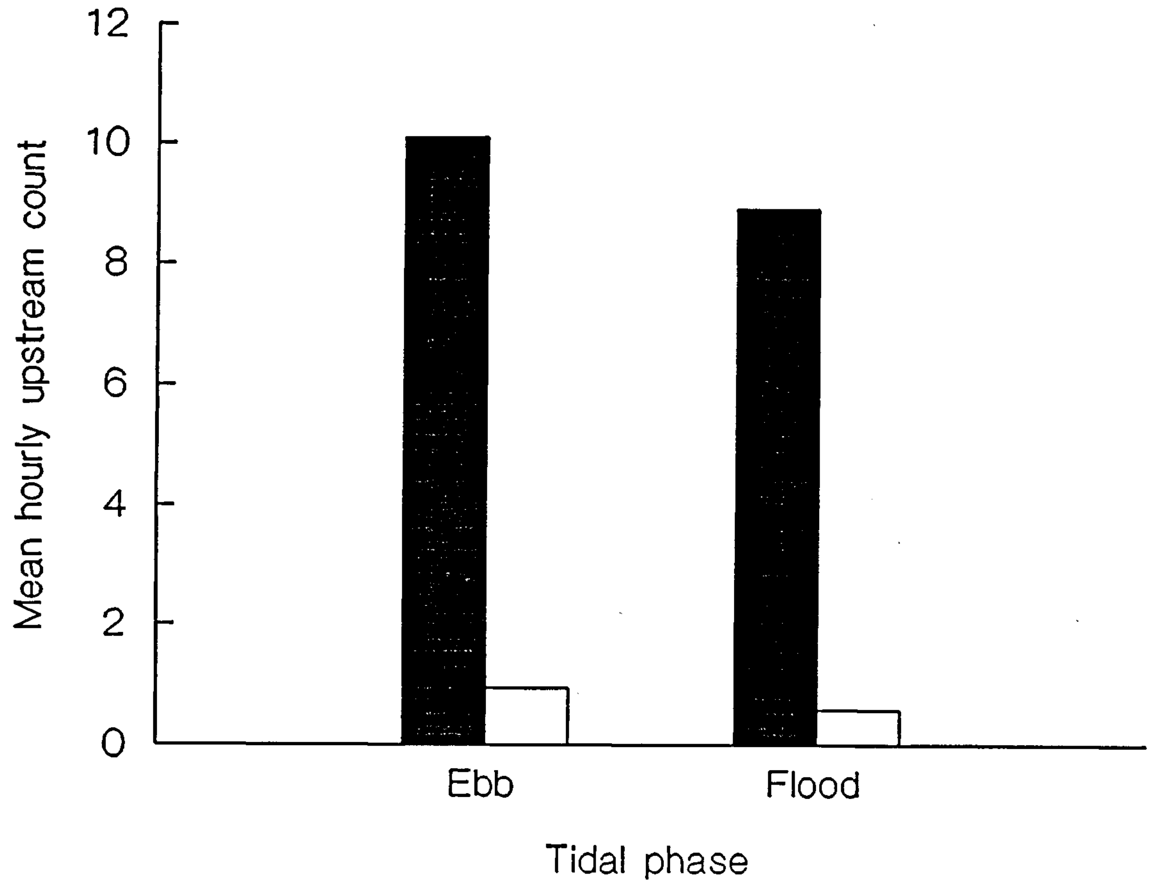

Figure 3 Mean hourly upstream count over the fish counter during the night (black boxes) and day (white boxes) in relation to tidal phase in Aberdeen harbour.

Figure 4 Frequency distribution of times when tagged fish were recorded moving past stations in relation to tidal phase.

a) Movement past the sonar buoy in the estuary
b) Movement past the ALS in the river

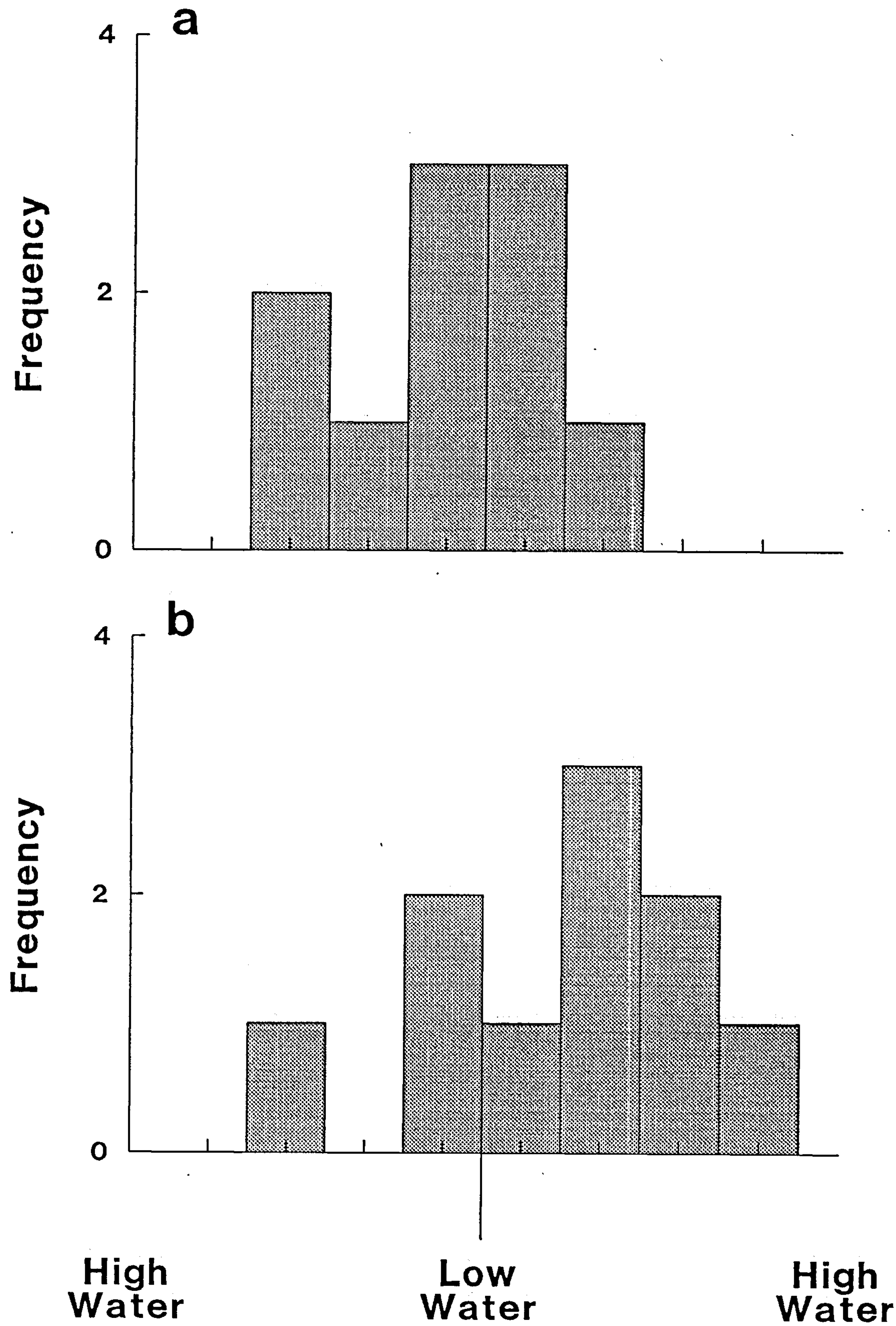

Figure 5 A theoretical analysis of how the association between the movements of a group of fish with tidal phase varies according to where along migration route the observations are made (see text for details).

a) The relationship between the mean resultant, r (a measure of how closely the data are concentrated together) and distance from a fixed starting point. The dotted line indicates the value of 'r' below which, at the 5% level of significance, there is deemed to be no significant concentration of observations around a particular tidal phase angle.

b) The relationship between the mean tidal phase angle around which the data are concentrated and distance along the migration route from a fixed starting point.