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ORIENTATION AND ENERGETIC EFFICIENCY IN THE OFFSHORE MOVEMENT OF RETURNING ATLANTIC SALMON

by

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ABSTRACT

During June and July 1979, two salmon and five grilse were tagged with acoustic transmitters and their movements recorded. Tidal flow was also directly measured using current driven drogues.

Offshore, movements of the fish were complex and strongly dependent on tidal currents. Subtraction of the tidal vectors however, showed that the true swimming course was consistently orientated to a particular direction for each fish, and independent of water currents.

Speed of movement through the water was averaged over each tidal phase for each fish tracked. These speeds were approximately equal to the most efficient swimming speed, defined as the speed at which energetic costs are lowest per unit distance travelled.

Rèsumè

Au cours de juin et de juillet 1979 on a attaché des emetteurs acoustiques à deux saumons et à cinq grilses pour enregistrer leurs mouvements. Le flux de la marée aussi a été mesuré directment en se servant d'ancres flottantes dirigées par le courant.

Au large, les mouvements des poissons étaient complexes, déterminés en grande partie par les courants de la marée. La soustraction des vecteurs de la marée cependant a montré que la route vraie de la nage pour chaque poisson s'est orientée conséquemment dans un sens particulier, et indépendante des courants dans l'eau.

La vitesse moyenne des mouvements à travers l'eau a été etablie pour chaque poisson qu on a suivi, pendant chaque phase de la marée. Ces vitesses étaient approximativement égales à la vitesse de nage ayant le meilleur rendement, c'est à dire, la vitesse à laquelle la consommation d'énergie est la plus basse pour chaque unité de distance parcourue. On discute ce résultat par rapport au temps qu il fout aux saumons rentrer à la rivière natale des régions lointaines où ils vont pour s'alimenter.

INTRODUCTION

The Atlantic salmon (Salmo salar L.) is spawned in freshwater and spends from one to three or four years of its adult life at sea where it maintains a very high rate of growth before returning again to freshwater to spawn. Although there is still some controversy concerning the homeward migration, the weight of evidence suggests that many of the fish which return do so from as far away as western Greenland and the Faroes and that these fish amy eventually return to the river of their birth.

Our investigations concern the final phase of this homeward journey where the returning salmon strike the coast of Scotland. Several fish were caught in coastal bag-nets during the summer of 1979, tagged with acoustic transmitters, released, and their subsequent movements examined. A previous report describing earlier observations, made in 1978, has already been published (Hawkins et al., 1979).

MATERIAL AND METHODS

The Study Area

The fish were captured in bag-nets at the Rockhall station of Messrs Joseph Johnston and Sons Ltd, some 8 km north of Montrose on the east coast of Scotland. They were released approximately 0.5 km offshore, in at least 10 m of water, and subsequently ranged up to 17 km offshore and as far north and south as Aberdeen and the Bell Rock, respectively, before tracking was suspended.

Tides in this area flow along a more or less north-south axis. Flooding to the north and ebbing to the south. One tidal cycle is completed in approximately 13 hours.

A more detailed description of the study area is given in Hawkins et al. (1979).

Tagging

The experimental fish was removed from the bag-nets and immediately placed in a black polythene bag containing a solution of MS222 in sea water (1 part MS222 in 10,000). When deeply sedated, the animal was transferred to a wooden board where it was measured and a sample of scales removed for later analysis. A conventional hydrostatic tag was inserted just in front of the dorsal fin and an acoustic transmitter gently pushed into the stomach.

The fish was kept for two to six hours in a cage on the sea bottom marked by a surface float. This period was to allow the fish to recover from the stress of capture and its subsequent treatment with anaesthetic. The fish was later released from the cage by passing a messenger weight down the float line from the surface to trigger a catch holding the door closed. The fish was allowed to swim from the cage in its own time and was subsequently tracked by two boats provided with tracking equipment.

Tracking

The acoustic transmitters were supplied by the Fisheries Laboratory, Lowestoft and emitted 1.5 ms long pulses at a nominal 75 kHz once every 1.5 seconds. They were cylindrical in shape with a diameter of 14.7 mm, and a length of 58 mm, weighing some 23 g in air and approximately 10 g in water. An external coat of hard epoxy resin and a cap of dental wax covering the switch terminals sealed the tag from the water.

The transmitter was tracked by means of a Lawson directional receiver operated from an inflatable boat powered by a 25 hp outboard engine. The inflatable kept station with the tracked fish while the second boat, a 27 foot launch, recorded the position of the inflatable and thus the fish at intervals of fifteen minutes.

The position of the vessel was fixed by means of a Decca Trisponder radio-navigational aid housed in the launch. The device provided the distance of the vessel from two stations on the mainland, each to an accuracy of within ± 3 m. Thus, by solving the simultaneous equations for two circles, the position of the fish on an arbitrary fixed rectangular grid was calculated. The tracking grid could be related to the Ordinance Survey grid system as the positions of both stations on the mainland were known relative to both grid systems.

Tidal flow was measured directly using the launch, the Decca Trisponder system and a series of drogues. The drogues were made from two aluminium sheets each 50 cm x 70 cm, and were cruciform in shape, suspended from an eight inch diameter trawl float by lines varying in length from 1 m to 15 m.

During the 15 minute periods between position fixes on the fish, one or two drogues were dropped near the fish and tracked from the launch. At these times the inflatable maintained contact with the fish. Position of the drogues at five minute intervals were determined by means of the Trisponder system. Tidal monitoring was carried out at least once every hour.

The tidal flow was generally measured at 1, 3, 5 and 10 m. Inspection of the results showed little change in the speed or direction of water flow with depth, this fact being supported by occasional measures taken with a direct reading current meter. We had no indication of the depth at which the tracked fish swam, but our own drift net observations, and work reported by Stasko et al. (1972) suggest that returning salmon in the open sea swim close to the surface. Drogue movements at either 1 m or 3 m were therefore taken as the best measures of tidal flow as it affected the salmon.

Data Analysis

The track of the fish was defined as the movement of the fish relative to the ground, and was simply the succession of fish positions given by the Trisponder system. A series of vectors, the track vectors, describing average speed and direction of fish movement between successive positions was calculated from the track.

Tidal vectors were calculated as the average speed and direction of movement of the drogues determined approximately once every hour. For times between each direct measurement of the tide, the vector was estimated assuming linear changes in speed and direction between measured flows.

The course vectors of the fish describe the movements of the fish relative to the water and were calculated by subtracting the appropriate tidal vector from each track vector. The course or heading of the fish was thus the direction in which the fish attempted to swim with the deflecting effects of tidal flows removed.

During the major part of each tidal phase, the speed and direction of tidal flow remained relatively constant. Thus linear interpolation between current measurements some one hour apart is a good estimator of tidal flow. Around periods of slack water however tidal speeds and direction changed much more rapidly and to a far greater extent. Our sampling over periods of slack water thus gave a less clear picture of tidal movements. As the fish course vectors were calculated from both fish track and tidal vectors, they were therefore especially open to error during periods of slack water. For this reason, slack water periods were removed from the data for some of the subsequent analyses by defining each phase of the tide as occurring between a period one hour after the estimated time of slack water and one hour before the estimated time of the next slack water.

Angular distributions of distance moved in each tidal phase by the fish on its track, on its course, and by the tide were calculated from the appropriate succession of vectors. These data were then plotted separately for each fish and for different tidal phases. To ease comparison of distances moved between tidal phases of differing lengths, distances were all corrected to correspond to a constant duration of tidal phase of four hours.

The significance of the mean direction in angular distributions was tested with the Rayleigh Test (Mardia, 1972), while differences in angular distributions was tested by the non-parametric Uniform Scores Test (Mardia, 1972).

RESULTS

Of the two salmon and five grilse tracked in 1979, none were observed entering rivers, and only rarely were they tracked close inshore. Our comments on their movements are thus largely restricted to behaviour in open water relatively distant from land and the effects of freshwater.

Orientation

Figure 1 shows the track and calculated course of one fish tracked over four tidal phases. The course was calculated by assuming an arbitrary starting point and calculating successive positions using in turn, each course vector and the time during which the fish remained on that vector. The complex pattern of movements shown in the track over the ground essentially disappeared with the calculation of the swimming course, where the deflecting influence of the tide was removed. Over the 21 hours of tracking and 3 changes of tide, Tennyson (Figure 1) maintained an approximately straight line course of ENE while his movement over the ground appeared far more complex. A similar behaviour was shown by the other fish.

Tennyson was subsequently recaptured six days after tracking was terminated in a sweep net on the River Spey some 200 km north and west of his last recorded position.

The tracking data also provides an opportunity for more quantative analysis of salmon orientation at sea. For each fish tracked over more than one full phase of the tide, fish track, fish course and tidal vectors were grouped with respect to tidal phase. The distances corresponding to each vector were then calculated and grouped into 20° sectors according to vector angle. Rose diagrams (Mardia, 1972) were produced where the radius of each segment was made proportional to the distance moved within the 20° sector. These angular distributions were calculated separately for fish track, fish course and tide for each fish and each phase of the tide. Figure 2 shows an example of a set of rose diagrams for Tennyson, the same fish illustrated in Figure 1.

Table 1 gives the statistics for the mean direction of course for each fish summed through all tidal phases. Such movement relative to the water shows a strong and consistent directional bias through all tidal phases for each fish. This is despite the fact that movement over the ground is in each case complex and apparently greatly influenced by the tidal currents.

The Uniform Scores Test (Mardia, 1972) was used to test for significant differences in the angular distributions. Table 2 gives the results of comparing fish track distributions between tidal phases for each fish. Table 3 gives the results of the same test on distribution of fish course.

Significant differences in fish movement relative both to ground and water exist between tidal phases. From Tables 2 and 3, however, each R^* value in Table 3 is lower than the corresponding value in Table 2. Variation in the direction of salmon movement over the ground can thus be seen to be magnified by the deflecting influence of tidal flow, whose direction and magnitude change over time.

Fish movement through the water also changes from one tidal phase to the next. There is some evidence from Table 3 however that this is not in direct response to the direction of tidal flow. Smaller values of R^* do not occur when distributions corresponding both to floods or ebbs are compared, but rather when comparison is between successive tidal phases.

Swimming Speed and Energetic Efficiency

For each fish tracked in 1979, fish length was converted to a weight using a relationship calculated specifically from salmon caught in the Montrose area at the appropriate time of the year. Data from Brett (1965) on the swimming performances of sockeye salmon (Oncorhyncus nerka) were then used to calculate the swimming costs of moving a constant distance of 1 km at a series of different swimming speeds. Figure 3 gives an example of such a cost curve for the fish TENNYSON. For each fish tracked, the mean observed speed of movement through the water was calculated separately for each tidal phase. The data are given in Table 4. The observed swimming speeds for TENNYSON are indicated on Figure 3.

If we define the most efficient swimming speed as that which provides the lowest energetic output per unit distance travelled, then all fish save one travelled either very close to or below their most efficient swimming speed. The remaining fish, TRISTAN, swam at approximately three times his calculated most efficient speed. This faster speed resulted however in an increase in cost per unit distance of only 19% (Table 4), due to the shallow slope of the curve to the right of the minima. TENNYSON on the other hand (Table 4), moving at just under one half his calculated most efficient speed incurred a maximum increased cost of 64% over the calculated minimum.

DISCUSSION

Orientation

The offshore movements of returning Atlantic salmon appear complex when viewed as a simple track over ground. With the removal of tidal effects, however, it becomes clear that the fish are maintaining a straight line course relative to the water and are deflected from this by tidal flow which changes both speed and direction periodically.

The fish course does change slowly with time though this change does not appear to be related to any tidal changes. The changes in course may reflect an inability by the fish to maintain a given course over a long period. It may also however indicate course changes which compensate for any drift which might change the position of the fish relative to some destination. To critically examine these hypotheses in more detail we would need to follow fish of known destination. So far, our observations do not allow us to suggest any particular sensory mechanism for the maintenance of a swimming course by the salmon.

Swimming Speed and Energetic Efficiency

All fish, save one, swam at speeds relative to the water which were very close to or below their calculated most efficient swimming speeds. Fish thus appear to minimise the energetic costs of their journey back to the river mouth rather than the time taken on that journey. However, to swim at speeds greater than the most efficient is proportionally less expensive in energy terms than swimming at slower speeds. Thus energy saving and travelling quickly are not necessarily incompatable. This is evident from Table 4, where TRIDENT swam at three times his most efficient swimming speed, but incurred no greater penalty in energy costs than did either TENNYSON or TEMPEST when swimming only slightly below their best speeds.

A slower speed may thus have advantages other than energetic saving, allowing perhaps the possibility of feeding en route or it may even be necessary for the setting and maintaining of a course. Distance from the home river may also affect the relative merits of different swimming speeds and go some way towards explaining the variability observed.

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TABLE 1 The mean direction and circular standard deviation of fish course summed over the total tracking period for each fish. Rayleigh test of circular uniformity (Mardia, 1972) critical value for $p = 0.001$, $2n\bar{R}^2 = 13.82$.

Fish	Mean Direction	Circular Standard Deviation (Degrees)	Rayleigh Test $2n\bar{R}^2$	Significance Level
TRIDENT	126.2 (SE)	24.7	12612	$p < 0.001$
THOR	133.4 (SE)	25.1	23190	$p < 0.001$
TEMPEST	205.8 (SSW)	35.2	14523	$p < 0.001$
TRISTAN	187.6 (S)	13.7	48571	$p < 0.001$
TENNYSON	61.0 (ENE)	44.2	12636	$p < 0.001$

TABLE 2 Comparison of angular distribution of fish movement over the ground (fish track) between tidal phases for each fish tracked for more than one phase of the tide. Critical value of R^* for $p = 0.001$, 13.82.

Fish	Tidal Phases Under Comparison			Uniform Scores Test R^*	Singificance Level
THOR	Flood1	v	Ebb1	124.65	$p < 0.001$
TEMPEST	Ebb1	v	Flood1	36.18	$p < 0.001$
	Ebb1	v	Ebb2	46.31	$p < 0.001$
	Flood1	v	Ebb2	42.83	$p < 0.001$
TRISTAN	Ebb1	v	Flood1	98.38	$p < 0.001$
TENNYSON	Flood1	v	Ebb1	50.90	$p < 0.001$
	Flood1	v	Flood2	33.15	$p < 0.001$
	Flood1	v	Ebb2	47.19	$p < 0.001$
	Ebb1	v	Flood2	81.75	$p < 0.001$
	Ebb1	v	Ebb2	52.37	$p < 0.001$
	Flood2	v	Ebb2	90.87	$p < 0.001$

TABLE 3 Comparison of angular distribution of fish movement through the water (fish course) between tidal phases for each fish tracked for more than one phase of the tide. Critical value of R* for $p = 0.05$, 5.99.

Fish	Tidal Phase Under Comparison	Uniform Scores Test R*	Significance Level
THOR	Flood1 v Ebb1	27.17	$p < 0.001$
TEMPEST	Ebb1 v Flood1	6.44	$p < 0.05$
	Ebb1 v Ebb2	29.80	$p < 0.001$
	Flood1 v Ebb2	13.82	$p < 0.01$
TRISTAN	Ebb1 v Flood1	2.96	NS
TENNYSON	Flood1 v Ebb1	3.93	NS
	Flood1 v Flood2	30.47	$p < 0.001$
	Flood1 v Ebb2	15.50	$p < 0.01$
	Ebb1 v Flood2	23.00	$p < 0.001$
	Ebb1 v Ebb2	11.82	$p < 0.01$
	Flood2 v Ebb2	12.41	$p < 0.01$

TABLE 4 Speed and the energetic cost of movement through the water for Atlantic salmon tracked in 1979

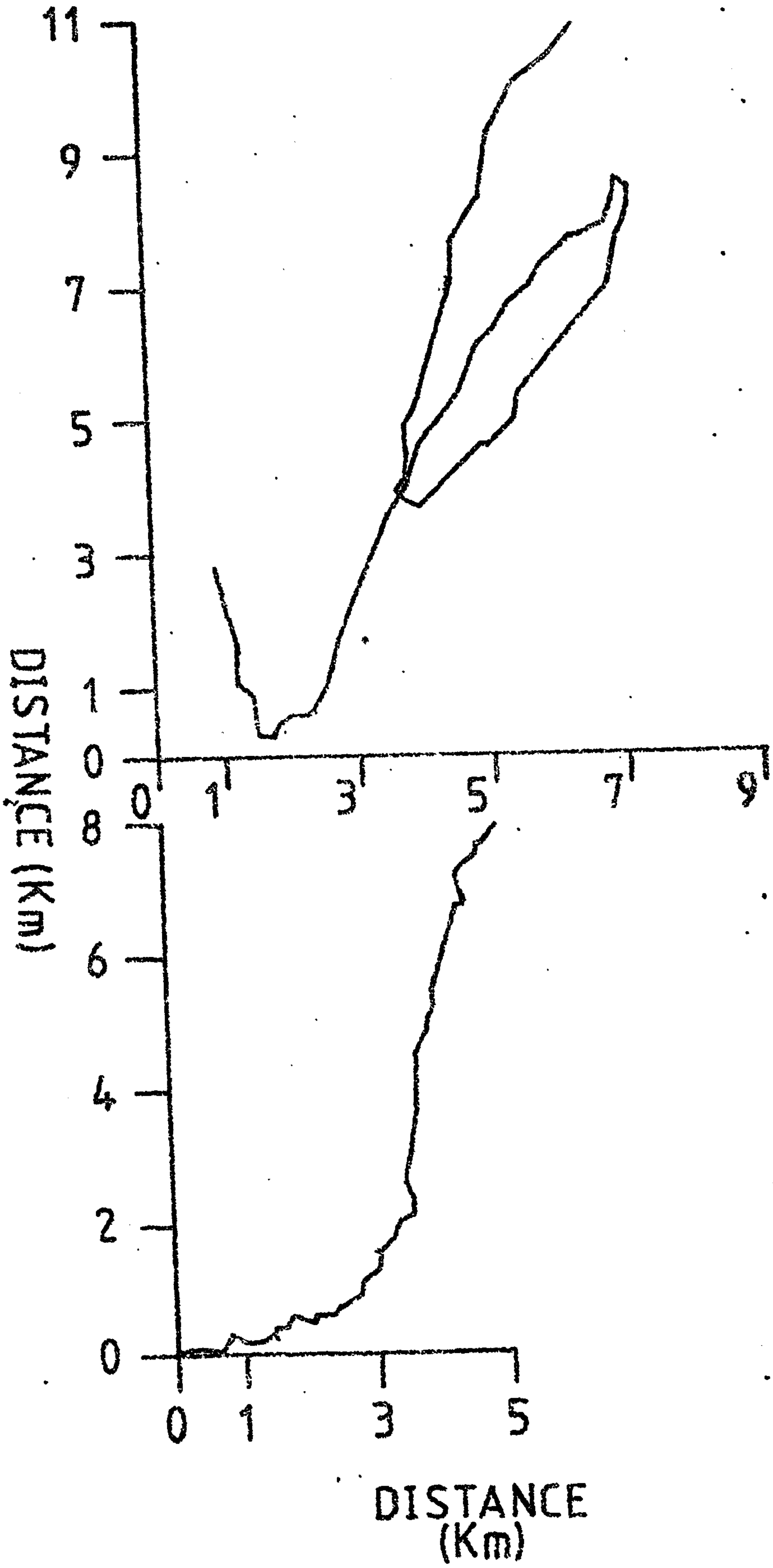
Fish	*Speed through the water (Body Lengths/sec)		*Cost of movement Mg O_2/Kg/Km		% Increase of Cost over Minimum
	(a)	(b)	(a)	(b)	
TRIDENT	0.54	0.54	56.59	56.59	0.0
THOR	0.65	0.51	50.91	49.59	2.7
	0.46	0.51	51.51	49.59	3.9
TEMPEST	0.35	0.59	83.49	66.12	26.3
	0.41	0.59	77.49	66.12	17.2
	0.36	0.59	84.48	66.12	27.8
TRISTAN	1.31	0.59	74.37	67.37	10.4
	1.55	0.59	80.51	67.39	19.5
TENNYSON	0.41	0.57	73.96	63.44	16.6
	0.24	0.57	103.78	63.44	63.6
	0.42	0.57	73.87	63.44	16.4
	0.27	0.57	92.52	63.44	45.8

*(a) Speed and energetic costs for fish tracked in 1979

(b) Speed and energetic costs at calculated most efficient swimming speeds

FIGURE 1

The track (upper) and calculated course (lower) of one grilse, TENNYSON, tracked over 21 hours.



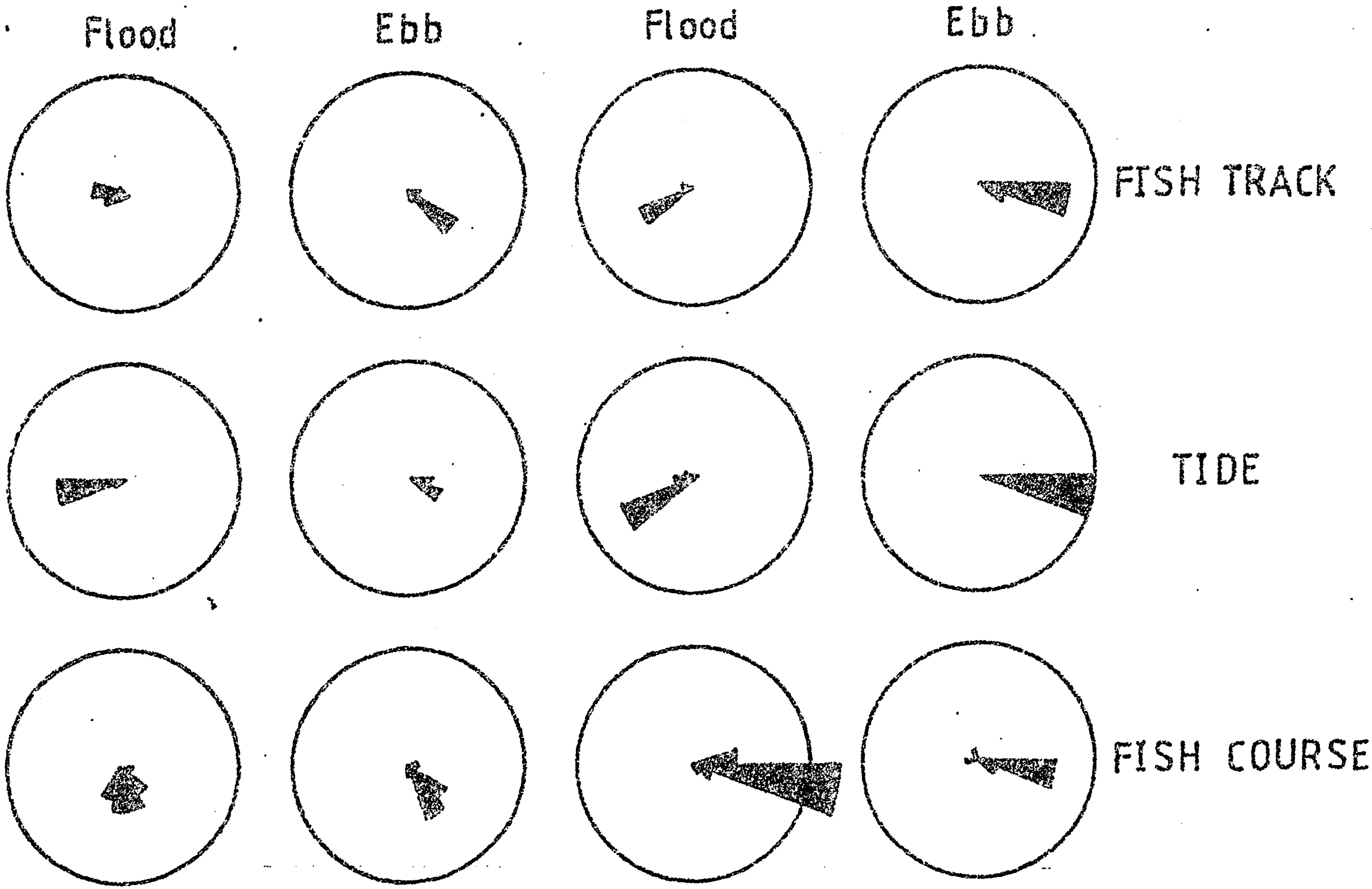


FIGURE 2 Angular distribution of the fish track, tide and fish course vectors for the grilse TENNYSON. In each circle, the radius of each 20 degree segment is proportional to the distance moved in that direction, corrected to a constant observation period of 4 hours. The circles are drawn at 8 km for fish track and tide, and 2 km for fish course.

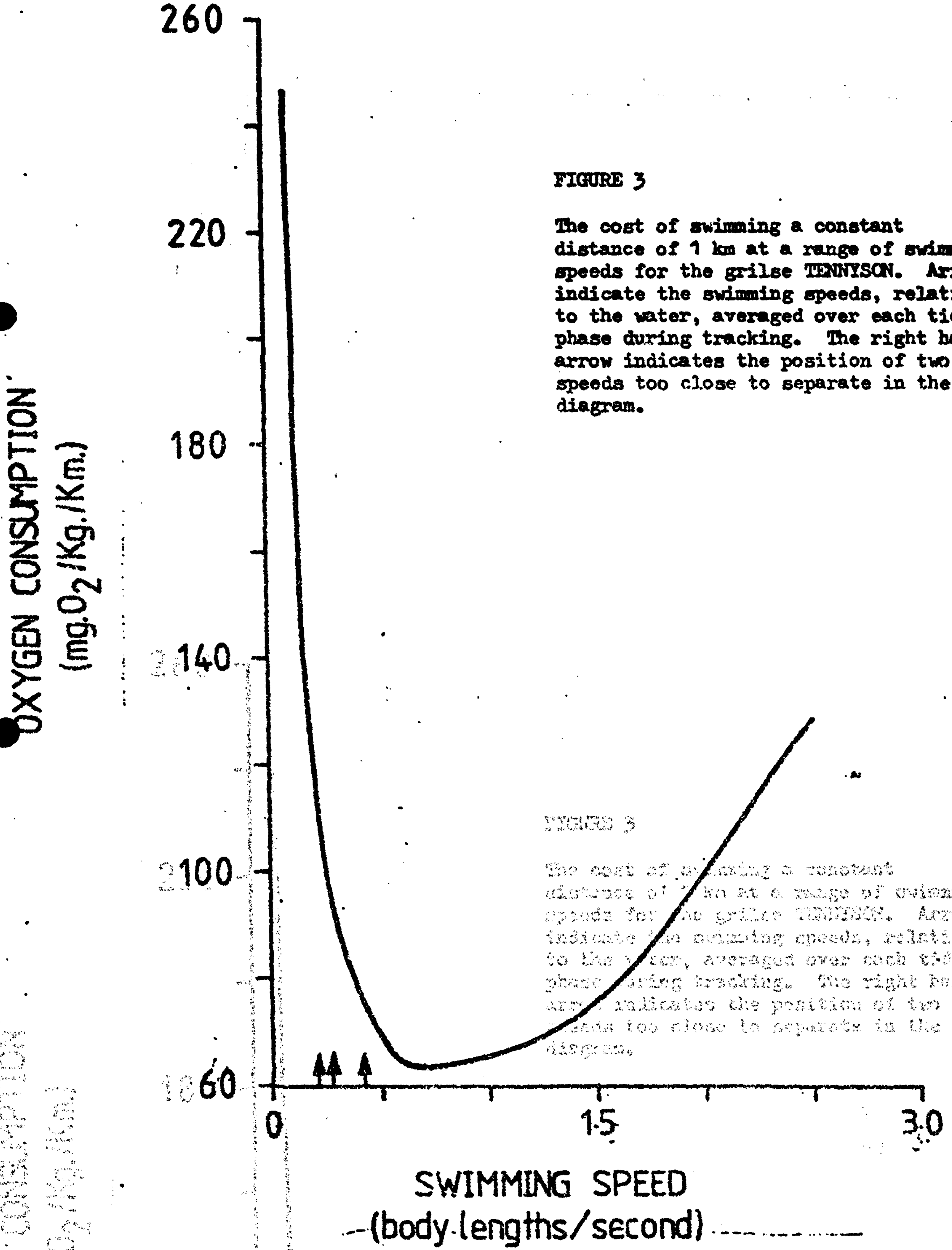


FIGURE 3

The cost of swimming a constant distance of 1 km at a range of swimming speeds for the grilse TENNYSON. Arrows indicate the swimming speeds, relative to the water, averaged over each tidal phase during tracking. The right hand arrow indicates the position of two speeds too close to separate in the diagram.