The Effect of Water Flow Rate on Bimodal Orientation of Juvenile Chum Salmon, *Oncorhynchus keta*

A wide variety of animals display compass orientation or directional preferences in radially symmetrical testing arenas. The orientation is generally unimodal, in a direction appropriate for migration or for naturally or artifically conditioned movement. However, in a number of cases animals orient bimodally, in the expected direction and approximately 180° away (e.g. fish: Groot 1965; Quinn & Brannon 1982; amphibians: Adler & Taylor 1981; reptiles: Landreth 1973; birds: Bingman 1981). This "back-azimuth" orientation may be caused by the animals' inability to distinguish directions along an axis, but experimental artifact and motivational conflict are difficult to rule out. The results of our study indicate that experimental techniques can play a role in generating bimodal orientation behaviour.

Juvenile chum salmon (*Oncorhynchus keta*) emerge from gravel nests in rivers and migrate downstream at night to salt water immediately or after a few days or weeks of freshwater residence. They then continue through bays and inlets to the ocean. Quinn & Groot (1983) found that young chum salmon from Conuma River, British Columbia, Canada showed southwesterly compass orientation in testing arenas during this early migration period. This directional preference is appropriate for reaching the ocean from the river mouth through Tlupana Inlet.

To investigate chum salmon orientation further, approximately 40,000 newly emerged Conuma River chum salmon fry were transferred to oval outdoor holding tanks on 10 March 1983. Each evening, 200 fry were placed in each of four outdoor uncovered cylindrical plastic tanks, 61 cm wide and 66 cm deep, filled with fresh water to a depth of 12 cm. Water entered the tanks via a central standpoint, and flowed out evenly through eight equidistant ports (Quinn & Groot 1983). Fry were placed in the tanks after sunset and allowed to move out into catch buckets at will until the water was turned off just before sunrise. During 10-25 March and 1-4 April, the water flow to each exit port was 6 litres/min, but during 27-31 March and 5-8 April the flow was reduced to 3 litres/min/pct. It is difficult to maintain uniform flow rates, but most flows were within 5% of the 3 and 6 litre/min averages. Sky conditions varied, but both overcast and clear skies were present during low and high flow rate tests.

The fry were more active (downstream movement) at the high flow rates: 91% of the 15,978 fry tested left the tanks in the high-flow-rate condition, versus 66% of the 6,373 fry tested at the low flow rate. At the high flow rate, orientation was unimodal and generally southward. The mean of the bearings of the individual fry was 182° (N = 14,504, r = 0.185, P < 0.001; Batschelet 1965). Second-order analysis (Batschelet 1978) of the means of the 20 nights of testing showed the same pattern (Fig. 1A). However, at the low flow rate the orientation calculated with unimodal statistics (N = 4,199, 260°, r = 0.045) was much weaker than the bimodal axis (14°/194°, r = 0.128, P < 0.001) calculated by doubling the angles (Batschelet 1965). Second-order analysis of the doubled angles also revealed non-random orientation along this axis (Fig. 1B).

The unimodal southerly orientation of chum fry at the high flow rate agrees generally with past results (Quinn & Groot 1983) and indicates that when rheotactic cues are equalized, chum salmon fry prefer to swim downstream in the compass direction appropriate for early marine migration. The change to bimodal orientation at the low water flow rate (with presumably no other change in sensory inputs) suggests that relatively subtle aspects of experimental conditions may influence the motivation of animals to orient in certain directions. In some situations, such as when animals are trained to the E-vector of polarized light (Auburn & Taylor 1979), bimodal orientation is expected, and does not indicate any experimental artifact. However, in other situations it is not clear why some animals move roughly 180° away from the expected direction. In the present study, the fact that a reduction in water flow was associated with bimodal orientation indicates that care must be exercised in interpreting bimodal orientation behaviour. This is particularly true in fishes, where rheotactic responses may change at different flow rates (Brannon 1972), and where riverine flow may influence fish to remain in the river or migrate to sea.

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**References**


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