



Quantifying behaviour of migratory fish: Application of signal detection theory to fisheries engineering

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ABSTRACT

Behavioural devices that attract or deflect migrating fish to preferred routes are used to enhance the efficiency of mechanical structures (e.g. screens at turbine and other intakes) or as an alternative to them when their application is deemed unviable. Fish response to stimuli (signals) encountered, and consequently the efficiency of these behavioural devices, can be highly variable. To further develop efficient behavioural screens and fish pass technology there is a need for a generic framework to (1) better understand fish response to environmental stimuli and causes of variation, and (2) quantify ability to detect stimuli and respond in a way deemed appropriate from a management perspective. This paper considers application of signal detection theory (SDT) to fish passage research, using downstream migrating juvenile salmonids as a model. Support is provided in the scientific literature for two key assumptions, that downstream migrants are able to exhibit volitional behaviour in response to stimuli encountered and that these behaviours can be interpreted by an observer to indicate the detection of a signal. Re-evaluation of available data highlights the temporal variability of decision making and elicitation of behaviour within and between individuals, and that sensitivity (d'), a measure of the ability to detect a signal (e.g. hydraulic gradient), increases with signal strength and when multimodal stimuli are presented. SDT is likely to provide a useful "first base" for understanding and quantifying fish behaviour in the development of screens and fish passes.

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1. Introduction

Mitigating environmental impacts of river, estuarine and coastal infrastructure development (e.g. for energy generation, water supply, and flood defence) is an important engineering challenge with considerable historic precedent (Katapodis and Williams, in press). From a fisheries perspective, mechanical screens block access to hazardous areas (e.g. turbine intakes and abstraction points) and guide fish to more benign and preferred routes (e.g. fish passes). On the one hand, fish behaviour can adversely impact the efficiency of screens (e.g. Russon et al., 2010) and fish passes (Kemp et al., 2008), whilst on the other can be manipulated to improve it (e.g. Johnson et al., 2000). A multitude of stimuli have been used to attract, repel and guide fish (Turnpenny et al., 1998), and include hydrodynamic features (e.g. those created by Louvers, Kynard and Buerkett, 1997), lights (e.g. continuous lights, Lowe, 1952; strobe lights, Konigson

et al., 2004; Richards et al., 2007), shade created by overhead cover (e.g. Greenberg et al., in press; Kemp et al., 2005a), pheromones (e.g. Bjerselius et al., 2000), electricity (e.g. Dawson et al., 2006), sound (e.g. Knudsen et al., 2005; Maes et al., 2004; Popper et al., 2004), air bubbles (e.g. Dawson et al., 2006), and combinations of these (e.g. air bubbles and sound, Welton et al., 2002; air bubbles and strobe light, Patrick et al., 1985).

Behavioural screens and guidance systems are useful when efficacy of traditional methods are limited, e.g. for repelling larval and juvenile life-stages that due to their small size cannot be easily screened by mechanical means alone. However, the efficiencies of behavioural devices, often described using simplistic metrics such as percentage deflection or attraction, can be highly variable (e.g. Welton et al., 2002) ranging from ineffective (e.g. Kynard and O'Leary, 1993) to high (e.g. >95% for guidance of shortnose sturgeon *Acipenser brevirostrum* and pallid sturgeon *Scaphirhynchus albus* by Louver arrays, Kynard and Horgan, 2001). Although the performance of mechanical systems designed to deflect migrating fish can be poor (see Calles et al., in press), as a generalization, the efficiency of behavioural screens tend to be lower (Turnpenny et al., 1998).

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There are several reasons for the intrinsic variability in the efficiency of behavioural screens. Behaviours vary between species (Schilt, 2007), reflecting multiple interspecific differences, e.g. life-history strategies, and between individuals, e.g. dependent on levels of boldness and general activity (Budaev and Zworykin, 2002). Within individuals, behaviours change over time, e.g. with stage of development (Huntingford, 1993) and physiological condition (Giorgi et al., 1988), motivational status (e.g. Colgan, 1993), habituation (Knudsen et al., 1992, 1997; Mueller et al., 1998), and prior experience and associated learning (Kieffer and Colgan, 1992). However, a lack of knowledge of the relationship between stimulus and response remains a key factor preventing progress in design of mitigation technology. Current understanding tends to be based on defining thresholds of stimulus detection. Acoustic screens, for example, are developed considering information provided by audiograms of target species obtained through invasive electrophysiological methods (e.g. Fay and Popper, 1974), by measuring the auditory brainstem response of immobilized fish (Kenyon et al., 1998), or by behavioural means based on the principles of classical (see review by Fay, 1988) or operant conditioning (e.g. Yan and Popper, 1992) which requires the training of the subject fish. These methods provide useful information on thresholds of discrimination, but are of limited use for defining the response of actively migrating wild fish that may or may not be inclined to respond to a stimulus when they detect it. To advance design of guidance devices there is a need to quantify wild fish behaviour, under experimental or field conditions, based on the ability to discriminate stimuli and to then respond in a manner deemed appropriate from a management perspective.

Signal detection theory (SDT) (Green and Swets, 1966; Tanner and Swets, 1954) provides a conceptual framework to explain and quantify behavioural performance of migratory fish, based on a process comprised of two components. First, SDT considers the relationship between magnitude and perceived intensity of a stimulus (signal) and the ability to discern between the signal and noise. Signal discrimination is primarily influenced by the magnitude of the signal and the amount of external and internal noise. Second, independent of discriminability, behavioural performance also depends on the individual's bias, i.e. the probability of eliciting a response on detecting the signal. From an applied perspective, the response may be that which is deemed appropriate by the fisheries manager, and reflects a shift from some "null" behaviour, e.g. swimming with the flow downstream, to an alternative, e.g. repelled to switch orientation and swim in the opposite direction. This paper is the first to consider the application of SDT to quantify fish ability to detect and respond to environmental signals (principally hydraulic factors) encountered during migration, and especially in association with passage at river infrastructure. The response of downstream migrating fish is considered because behaviour, rather than swimming capability, is likely to be the key determinant of migration trajectory assuming movement is not by obligatory passive means. Two key assumptions and two key predictions are made. The first assumption is that downstream migration is not obliged to be passive and fish will exhibit volitional behaviour in response to signals encountered. The second is that downstream migrating fish will exhibit behaviours that "indicate" detection of signals that can be observed and interpreted. It is then predicted that decision making and subsequent behavioural response will vary between and within individuals over time (e.g. with acclimation), and that discriminability will vary with availability of information and signal strength. Evidence from the literature and recent experimental research is reviewed in support or contradiction of the assumptions and predictions, and requirements for future research are identified.

		RESPONSE	
		YES	NO
SIGNAL	PRESENT	HIT: <i>Correct response</i>	MISS: <i>Incorrect response</i>
	ABSENT	FALSE ALARM: <i>Incorrect response</i>	CORRECT NON-RESPONSE: <i>Correct response</i>

Fig. 1. Four potential signal-response outcomes that may result in the presence or absence of a specific environmental stimulus.

2. Signal detection theory: the concept applied to the behavioural ecology of migratory fish and fisheries engineering

Nearly all decisions are based on information acquired in the presence of uncertainty (Heeger, 1997) and depend on two independent components, (a) information-processing and (b) decision-making/response-generating (Green and Swets, 1966). A migrating fish may encounter a multitude of abiotic (e.g. hydraulic factors such as velocity gradients, shear, and turbulence, and non-hydraulic variables such as sound, light or overhead cover) or biotic (e.g. presence of a predator, potential mate, or competing conspecific) environmental stimuli (signals) to which it may exhibit a behavioural response. At any given point during the migration a particular signal is either present or is not, and the subject fish will detect it and respond (in a way that is deemed appropriate from a fisheries management perspective, e.g. repelled or attracted) or it will not. Thus there are four possible signal-response outcomes (Fig. 1) reflecting both components of the decision making process: (1) the signal is present and the fish detects it and elicits a response (*hit*); (2) the signal is present but the fish elicits no response independent of detection (*miss*); (3) the signal is absent yet the fish elicits a response (*false alarm*); and (4) the signal is absent and the fish elicits no response, here termed *correct non-response* rather than *correct rejection* frequently referred to in the literature. The term *rejection* will be later applied to describe a scenario in which a fish swims in the opposite direction to a stimulus having encountered it (i.e. which may thus be considered a *hit*).

The ability to elicit a response or non-response may be considered in terms of behavioural performance (e.g. Steckler, 2001) based on the two components described. The probability of making a correct decision (*hit* or *correct non-response*) is influenced by the ability to acquire sufficient information, the first component, and individual bias, the second. SDT provides measures of the information-processing and decision-making components of the behavioural model.

2.1. Information-processing

The probability of making a correct decision partially depends on degree of uncertainty, referred to as external (exogenous) and internal (endogenous) noise (Heeger, 1997). For example, the ability of a fish to detect a spatial gradient of water motion (see Nestler et al., 2008) over a submerged structure will be influenced by the amount of background fluctuation in velocities, i.e. the external noise (see Bassett et al., 2006 for discussion of interspecific variation in sensitivity of the lateral line system). Internal noise relates

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