SIMULATING MIGRATION BEHAVIOUR AND

METABOLIC POWER CONSUMPTION

OF UP-RIVER MIGRATING SOCKEYE SALMON

IN THE FRASER RIVER, BC

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Introduction

Priede (1985) defines two types of selection pressures that are likely to be important in defining an animal's fitness. Type-1 selection is driven by energy conserving behaviours that operate across relatively extended time scales (days to weeks). These behaviours are important as a means to achieve high energy efficiency, thus leading to more energy diverted to metabolic processes that directly influence fitness. Type-2 selection is driven by fine time scale power budgeting (seconds to minutes), where the organism is faced with a defined metabolic scope which serves to limit power consumption at critical points through the organism's life history. Departures from this defined scope in nature result in increased risks of mortality. Adult Pacific salmon from some stocks presumably are influenced by both types of selection as a result of their costly river migration.

Most efforts at describing adapted behaviours in these fish have involved defining optimal swim speeds that minimize cost of transport (Weihs 1973; Ware 1975). We contend that these examples, along with the examples discussed earlier, are appropriate for investigating type-1 selection, but ignores finer time scale power budgeting implicit in type-2 selection. Swimming bursts measured at the scale of seconds occur routinely in these fish in the field (Hinch and Rand, 1998) and, given that energy costs are a power function of swim speed, these active periods can be inordinately expensive. By coupling the use of electromyogram (EMG) telemetry with simulation modeling, it is possible to generate more accurate measures of energetic costs in situ. In this paper we explore behavioural patterns measured across a broadly defined temporal scale (seconds to weeks) to compare the relative importance of both types of selection operating on energy efficiency during river migration.

We developed a simulation model that accounts for power consumption of upriver migrating sockeye salmon in the Fraser River. Our objective in this modeling study was (1) to test whether averaging over the variability observed in swim speeds introduces a significant bias in predictions of true costs to migrating fish, (2) to describe the fates of stored metabolic energy during the course of the river migration, including an evaluation of the importance of anaerobic costs from burst swimming and defining the full range of power consumed for activity in the field, and (3) to conduct error and risk analyses on the model to rank parameters with respect to their sensitivity, and define risks of increased mortality resulting from energy depletion for the average migrant in any given year based on the natural variability of environmental conditions in the river.

Methods

We constructed a simulation model to account for energetic losses resulting from basal and active metabolism during the river spawning migration in Early Stuart sockeye salmon in the Fraser River. The model also accounts for energy flow to maturing gonads. We refined existing bioenergetic models for sockeye salmon to represent the adult migrants in this study. Two different model configurations were developed: 1) a daily time step model that relied on a daily mean swim speed to estimate activity costs, and 2) a finer time scale model (5 s) that conforms more closely to the sampling rate of the EMG tags used in the field study (Hinch and Rand 1998). We tested the model against energy use data collected through tissue analyses on adults at different points along the migration route during 1956. We summarized the results of this simulation by partitioning the fates of stored energy between basal metabolism, active metabolism and gonad development. We conducted Monte Carlo simulations to determine which parameters were most sensitive in the model. Further, we conducted a risk analysis to help determine the relative mortality risk incurred by adults over the past 44 years given variability in return timing, size at maturity, and variability in river conditions (namely, discharge and water temperature).

Results and Discussion

The most accurate prediction of energy expenditure was obtained by expressing activity as a fine-time scale (5 s) stochastic process. By imposing a daily-time step, predictions of energy use were considerably lower than observed energy use, suggesting the practice of modeling field energetics at a daily-time scale, particularly for relatively active fish, may render dubious results. Daily mean power consumption through the Fraser River Canyon by the average successful migrant was circa 20 W, about four-fold higher than for less constricted reaches. Power consumption predicted at fine-time scales ranged from < 1 W (0.1 body lengths s^{-1}) during periods of reduced activity to 1700 W (8 body lengths s^{-1}) during bursts while navigating through turbulent canyon reaches. Activity dominated the energy budget of these salmon migrants. For our calibration run, 84% of stored energy was consumed by locomotor costs, while less than 20% was consumed by standard metabolism and gonad development. Through Monte Carlo simulations representing environmental variability observed during 1950-94, we determined 8% of the salmon runs during this time resulted in a high risk of exhaustion for the average migrant that could lead to elevated in-river mortality.

Results from our error analyses helped reveal important interactions between behaviour and energetics of sockeye salmon that have relevance to life history and evolutionary strategies for this species. Our results suggest that selective pressures may operate strongly on the behaviours that influence fine time scale power budgeting while enroute to the spawning grounds. This is reflected in the sensitivity of model predictions of energy use to the parameter values that defined the upper limit to the swim speed distribution. These selective pressures, referred to as type-2 by Priede (1985, see our Introduction), would help define the frequency and magnitude of bursts performed by these salmon as they progress to the spawning grounds. While these bursts appear to be necessary to successfully navigate through some of the more difficult reaches, our results suggest that there must exist strong selective pressures to minimize the frequency and reduce the absolute magnitude of these bursts to avoid risk of energy exhaustion. Fish do appear to restrict these expensive bursts, particularly those that exceed 80% of Ucrit, to difficult reaches within the Fraser River Canyon and Hell's Gate. If the fish exceed their metabolic scope, periods of stress can ensue that lead to hyperactivity and, ultimately, death (Black 1958; Wood et al. 1983). Hinch and Bratty (2000) have recently shown with EMG telemetry that sockeye that successfully ascended Hell's Gate swam at speeds that approximated their metabolic optima, whereas migrants who attempted to ascend but failed and died all swam at speeds that vastly exceeded optimal speeds. These results suggest that these fish are operating close to a physiological threshold, which may necessitate strong selection that would serve to fine-tune burst swimming behaviour.

Type-1 selection, as defined by Preide (1985, see our Introduction), appears to also play a role in defining energy efficiency of migration in this species. In particular, the mean swim speed defined in the model and the parameters that governed the relationship between mean swim speed and river discharge levels were all important based on the results of our error analysis. This suggests that reducing mean swim speeds in general, or reducing swim speeds under conditions of high river discharge, can be adaptive and result in higher energy efficiency during migration. Over an evolutionary time scale there must be some dynamic equilibrium between expanding field activity scope that allows for marginal increases in power to navigate through difficult reaches (type-2 selection) and more conservative locomotor behaviours that result in longer term savings in energy (type-1 selection).

How can this model be implemented into management? The regulatory body charged with managing these stocks, Fisheries and Oceans Canada (FOC), have adopted a risk-averse strategy for managing B.C. salmon (Blewett et al. 1996). Most of the regulatory effort by FOC is oriented toward managing harvest rates on these stocks as a means to achieve target escapement goals. We feel that it is critical for managers to realize that, while harvest is likely to represent the dominant source of mortality on these stocks in most years, in some years significant "natural" mortality may occur resulting from difficulties encountered during migration. Although we looked at only early Stuart stock in our analysis, it is reasonable to assume that these risks may also be important for other stocks as well. Although much uncertainty still exists in translating our risk index to an explicit mortality rate, we emphasize that this mortality risk should be included as a factor in pre- and in-season management during years where difficult passage conditions are expected. For example, when model predictions suggest high natural mortality risk for the average migrant in a particular year, harvest could be adjusted to reduce total fishing mortality, thus allowing more fish to successfully reach the spawning grounds.

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