AM. ZOOLOGIST, 11:99-113 (1971).

Energetic Responses of Salmon to Temperature. A Study of Some Thermal Relations in the Physiology and Freshwater Ecology of Sockeye Salmon (*Oncorhynchus nerka*)

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SYNOPSIS. Studies on the relation of temperature to tolerance, preference, metabolic rate, performance, circulation, and growth of sockeye salmon all point to a physiological optimum in the region of 15°C. Natural occurrence is limited in time and space at temperatures above 18°C despite being able to tolerate 24°C. Forms of physiological inadequacy can be demonstrated which account for such restrictions in distribution. Predictive power for locating and accounting for concentrations of young fish in thermally stratified lakes appeared to provide "proof" for the controlling influence of the physiological optimum temperature. Early literature on the ecology of sockeye supported this view. Recent studies using midwater trawls and sonar detection reveal a diurnal behavior pattern which points to a more subtle interaction of biotic and abiotic factors governing vertical distribution in which the controlling force appears to be bioenergetic efficiency. It is concluded that a mechanism of behavioral thermoregulation has evolved which favorably balances daily metabolic expenditures in order to conserve energy when food is limited.

INTRODUCTION

It is the purpose of this study to examine some of the physiological and ecological relations of young sockeye salmon, *Oncorhynchus nerka*, during lake residence, and to explore the extent to which temperature-dependent responses can be placed in biological context.

With the exception of some remarkable homeothermic adaptations which have been reported for the post-juvenile stage of a few large, fast-swimming fish (Carey and Teal, 1969*a*,*b*), the vast majority of fishes are strict thermal conformers (Fry, 1968). They may be classed as obligate poikilotherms or ectotherms, being highly heat conductive without producing sufficient metabolic heat even when active, to overcome rapid loss through the gills and epidermis. Since they, like present-day homeotherms, have had just as long to evolve adaptive thermal mechanisms, it is not surprising to find a variety of response systems which permit measures of escape from the potentially restrictive influence of complete temperature dependence. These involve cellular and systemic adaptations commonly called resistance adaptation, acclimation, summation, and compensation (See reviews of Bullock, 1955; Fry, 1958, 1968; Precht, 1967; Brett, 1970*b*). By comparison, however, these are no more than limited steps towards the temperature freedom which a fully regulated, homeostatic state provides—a state which has been achieved by most fish in relation to such environmental factors as salinity, oxygen, pH, and hydrostatic buoyancy. It is no wonder then that among the abiotic environmental factors temperature has been labelled the ecological master factor.

A comprehensive study of thermal responses in sockeye salmon has been conducted during the past two decades in our laboratory, stimulated lately by exploring techniques of environmental manipulation to enhance growth, and further by the common threat of elevated temperatures

I am particularly indebted to Dr. D. W. Narver for early discussions of the possible hypotheses which would account for the sockeye behavior. This stimulated the research program of Mr. R. Biette who, under the direction of Dr. Glen Geen of the Department of Zoology, Simon Fraser University, is conducting the searching enquiry necessary for any ultimate proof.

During the formulation of this paper Mr. J. G. McDonald has been most helpful in elaborating on the patterns of sockeye behavior and examining the deductions formulated.