

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, 1969a,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

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. C. McDonald has been most helpful in elaborating on the patterns of sockeye behavior and examining the deductions formulated.

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, 1970b). 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

TABLE 1. *Physiological responses of sockeye salmon to increasing acclimation temperature (Brett, 1952, 1964, 1970c; Brett and Higgs, 1970; Brett et al., 1969; Davis, 1968).*

Function	No.	Figure	Aspect	Response			Optimum Temp. °C (± 10% response)
				Continuous increase	Inflects down	Upper plateau	
Tolerance	1	1	Upper lethal temperature			x	—
	2	1	Lower lethal temperature	x			—
Preference	3	1	Selected temperature		x	?	15 ± 5
Metabolism	4	2A	Standard metabolic rate	x			—
	5	2A	Active metabolic rate		x		15 $\begin{smallmatrix} +10 \\ -2 \end{smallmatrix}$
	6	2B	Metabolic scope		x		15 $\begin{smallmatrix} +5 \\ -2 \end{smallmatrix}$
	7	2B	Locomotor metabolic demand	x			—
	8	2C	Oxygen-debt load		x		15 $\begin{smallmatrix} +3 \\ -2 \end{smallmatrix}$
Performance	9	2D	Maximum sustained speed		x		15 $\begin{smallmatrix} +10 \\ -7 \end{smallmatrix}$
	10	2D	Maximum volitional speed		x		15 $\begin{smallmatrix} +2 \\ -3 \end{smallmatrix}$
	11	2C	Post-fatigue death	x			—
Growth	12	3A	Growth rate (excess ration)		x		15 ± 2
	13	3B	Growth rate (restricted ration)		x		15 → 5 ± 2
	14	5A	Conversion efficiency (all rations)		x		11.5 ± 4
Appetite	15	3C	Voluntary food intake		x		17 $\begin{smallmatrix} +5 \\ -6 \end{smallmatrix}$
Digestion	16	3D	Gastric evacuation rate	x		?	—
Circulation	17	4A	Resting heart rate	x			—
	18	4A	Active heart rate	x			—
	19	4B	Resting blood pressure		x		15 $\begin{smallmatrix} +3 \\ -4 \end{smallmatrix}$
	20	4B	Active blood pressure		x		15 $\begin{smallmatrix} +3 \\ -4 \end{smallmatrix}$
	21	4C	Resting cardiac output	x			—
	22	4C	Active cardiac output	x			—
	23	4D	Resting cardiac work	x		?	—
	24	4D	Active cardiac work		x		15 $\begin{smallmatrix} +6 \\ -2 \end{smallmatrix}$
	25	5C	Cardiac scope		x		15 $\begin{smallmatrix} +5 \\ -3 \end{smallmatrix}$
TOTAL	25	% Type Response		10 (40%)	14 (56%)	1 (4%)	
SUBTOTAL	14	Inflects, with optimum		$\left\{ \begin{array}{l} \text{above } 15^{\circ}\text{C} = 1 (7\%) \\ \text{at } 15^{\circ}\text{C} = 11 (79\%) \\ \text{below } 15^{\circ}\text{C} = 2 (14\%) \end{array} \right.$			

(thermal pollution) and interaction with toxic wastes. Contemporary investigations have proceeded on the freshwater ecology of this species, stimulated in this case by a need for improved understanding of the production and early survival of this economically valuable species. As a result it is possible to examine in some depth the physiological and ecological relations. These will be considered in broad terms, followed by a more detailed examination of the possible causal mechanisms account-

ing for vertical migration during the months when lakes are thermally stratified.

PHYSIOLOGICAL DESCRIPTION

The various physiological responses of sockeye salmon to increasing acclimation temperature have been assembled in Table 1. In the main, these deal with whole organism responses rather than organ systems, and reflect the area of greatest interest, physiological ecology. However, it

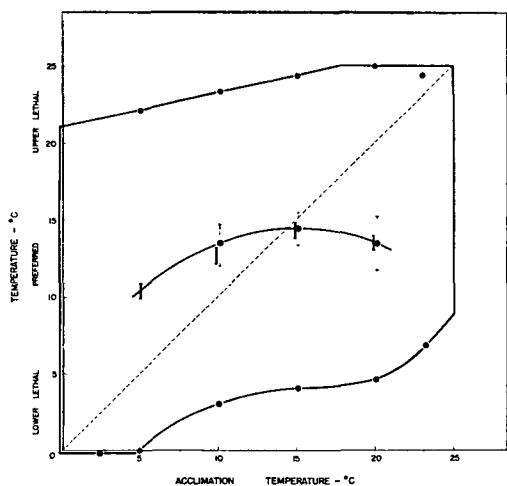


FIG. 1. Thermal tolerance and preferred temperature of young sockeye in relation to acclimation temperature. (From Brett, 1952).

must be admitted that although the choice has been influenced by the interests of resource management, it forms a fairly arbitrary assemblage reflecting personal curiosity without any other bias in favor of any particular physiological system. This is important because some simple statistical accounting of the rate functions has been performed.

Before analyzing the contents of Table I, some examination of the *basic trends* of response to temperature is desirable without dwelling on the details. With the exception of tolerance and preference (Fig. 1), the other responses have been grouped where possible to assemble interdependent and/or like functions, *e.g.*, metabolism with performance (Fig. 2), growth with food-intake and digestion rate (Fig. 3).

Tolerance and preference (Fig. 1). Both the upper and lower lethal temperatures show a continuous increase over most of the acclimation range. An upper plateau occurs for the high lethals, a feature which is not uncommon among fishes (Fry, 1968). There appears to be a corresponding lower plateau for the low lethals, just below 0°C, an area which can be explored only in saltwater-tolerant species. All other sustained functions can obviously be maintained only within the tolerance zone.

The preferred temperature rises to a

broad optimum, inflecting slightly downwards above an acclimation temperature of 15°C. Preferred temperatures have been shown to follow a variety of trends leading to a classification of responses, among which the above is Type 1 (Zahn, 1962). In this case the optimum happens to be the same as the "ultimate" preferred temperature, in the sense of Fry's (1947) concept where the selected temperature equals the acclimation temperature.

Metabolism and performance (Fig. 2). Standard or resting metabolic rate displays the almost universal characteristic of continuous increase with temperature (lowest curve in Fig. 2A). By comparison the active rate reaches an optimum at 15°C decreasing thereafter in a slow decline to 25°C, the upper lethal temperature (Fig. 2A). The presence of an optimum and downward deflection is mirrored in the metabolic scope (Fig. 2B) and performance curve (Fig. 2D), and is somewhat more pronounced in the tolerable levels of oxygen-debt (Fig. 2C).

A rather surprising relation is revealed by the data depicting locomotor metabolic costs (Fig. 2B). These exponential curves, relating rate of oxygen consumption to acclimation temperature, decrease in slope with increasing swimming speed, approaching zero slope at a speed of about 4 L/sec ($Q_{10} = 1$). This means that burst speeds are virtually *independent* of temperature. Rapidity of escape or attack is therefore not a direct function of temperature, a biological circumstance of considerable significance.

Growth, food-intake, and digestion rate (Fig. 3). Young, small sockeye show a sharp growth optimum at 15°C; the growth curve flattens with increasing size and age (Fig. 3A). A progressive shift to a lower temperature (15° to 5°C) occurs in the growth optimum as the quantity of food is restricted (Fig. 3B).

Maximum food-intake also shows an optimum broadly related around an apex at about 17°C (Fig. 3C). Appetite is completely inhibited at 24°C.

Digestion rate, the reciprocal of time to a given state of gastric evacuation, can be

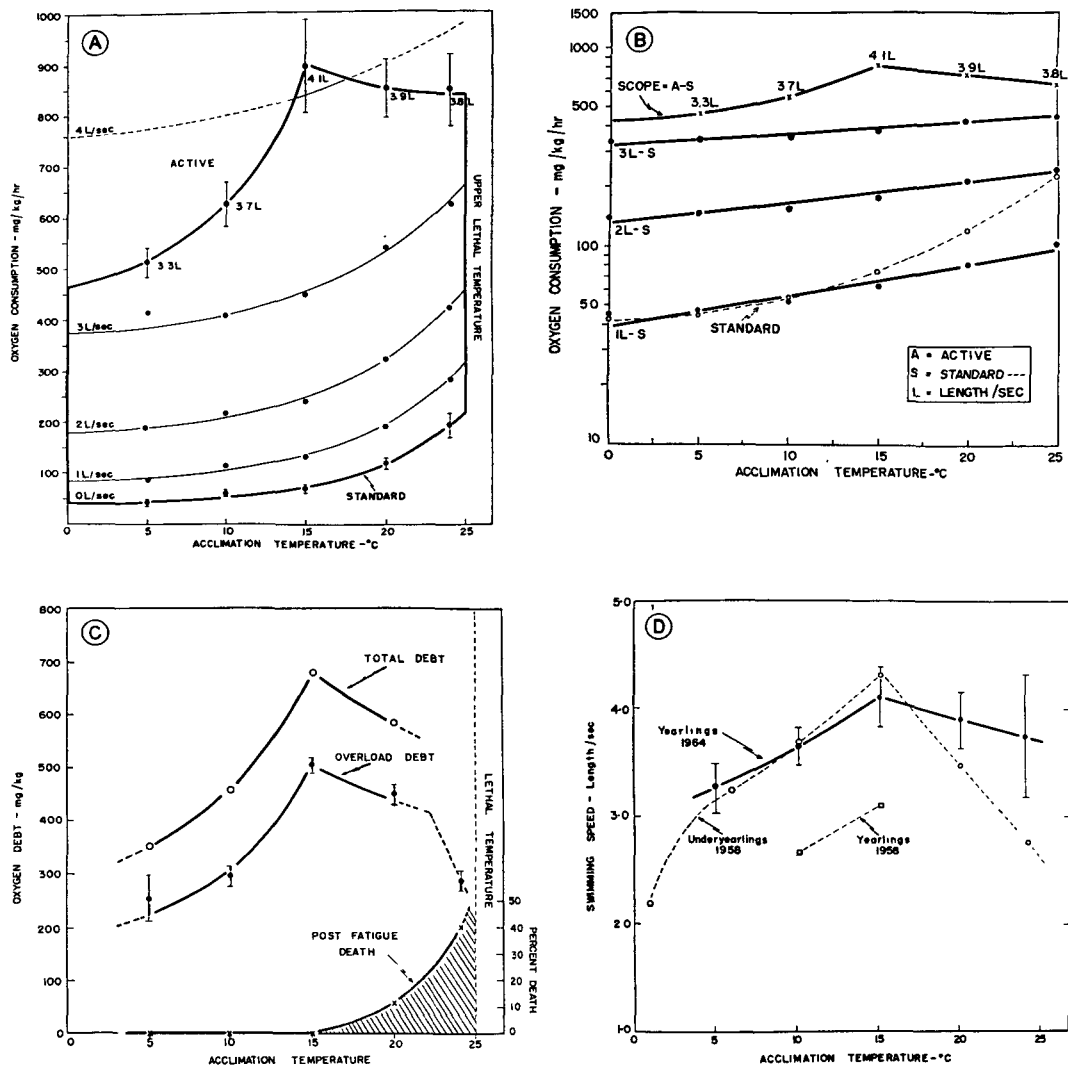


FIG. 2. Metabolic rates and performance in relation to acclimation temperature. *A* shows total oxygen consumption at various swimming speeds (fish lengths/sec); *B* shows locomotor metabolic demand (total minus standard) and metabolic

scope (active minus standard); *C* is the tolerable oxygen-debt and extent of post-fatigue death; *D* shows maximum sustained speed (solid) and volitional speed (dotted). (From Brett, 1964).

seen (Fig. 3D) to increase over most of the temperature scale, with a suggestion of flattening off at the highest temperature studied (23°C).

Circulation (Fig. 4). Heart rate and cardiac output for resting conditions (after 12 hours in a respirometer tube, not swimming) and maximum sustained activity both show a continuous increase with temperature (Fig. 1A,C). This is in contrast to the mean blood pressures and cal-

culated cardiac work which show temperature optima at 15°C or slightly higher (as interpreted by D. J. Randall, pers. comm.; Fig. 4B,D). Cardiac work (ergs/min) was calculated as the product of output (ml/min) times mean pressure (mm Hg). Cardiac output was applied rather than heart rate as is used for calculating cardiac work in mammals which, unlike fish, have a relatively constant stroke volume (Bing, 1965).

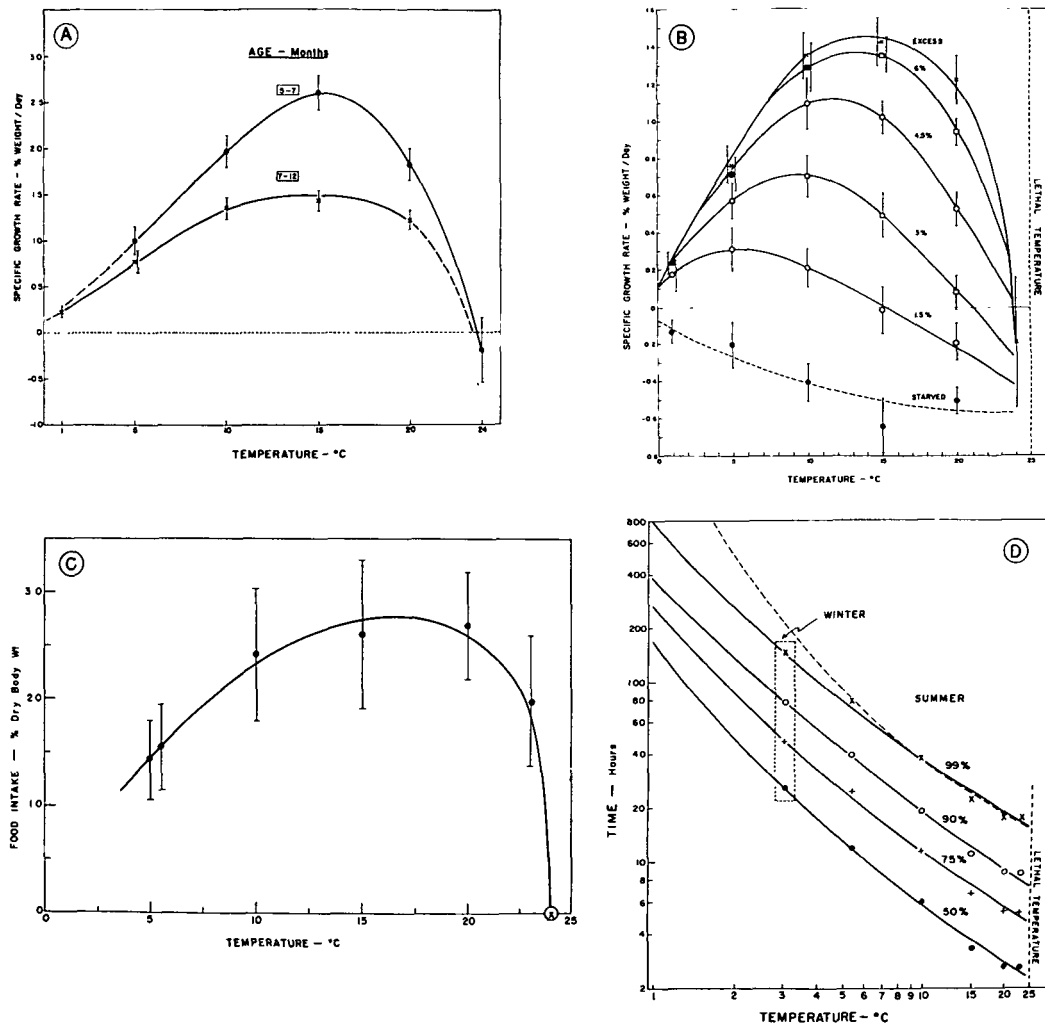


FIG. 3. Growth, food-intake (appetite), and rate of gastric evacuation in relation to acclimation temperature. *A* relates to excess ration at two ages, *B* to excess and restricted rations, *C* to daily satiation intake, and *D* shows the time required to

digest pelleted feed—the reciprocal ($1/\text{time}$) would give the rate, with the lines sweeping up the graph. (From Brett, *et al.*, 1969; Brett and Higgs, 1970).

Interdependent and type responses (Fig. 5). When ration and growth rate are both measured, gross conversion efficiency (% flesh from food) can be calculated and plotted as isopleths (Fig. 5A). The relation provides a center of maximum efficiency indicating the best combination of temperature and ration—an “interaction optimum” peaking at 11.5°C.

By examining the combination of conversion efficiency, growth rate, maximum meal size, and digestion rate (Fig. 5B), the

suppressing effect of low temperature is apparent in all cases. Although rate of digestion continues to increase above 15°C, conversion efficiency begins to decline, falling off precipitously above 20°C, as does appetite. This results in a corresponding decline of growth which is completely blocked at 24°C (Brett and Higgs, 1970).

The parallel interdependence of performance, metabolic scope, and cardiac scope is to be expected (Fig. 5C). Since the drag associated with swimming in-

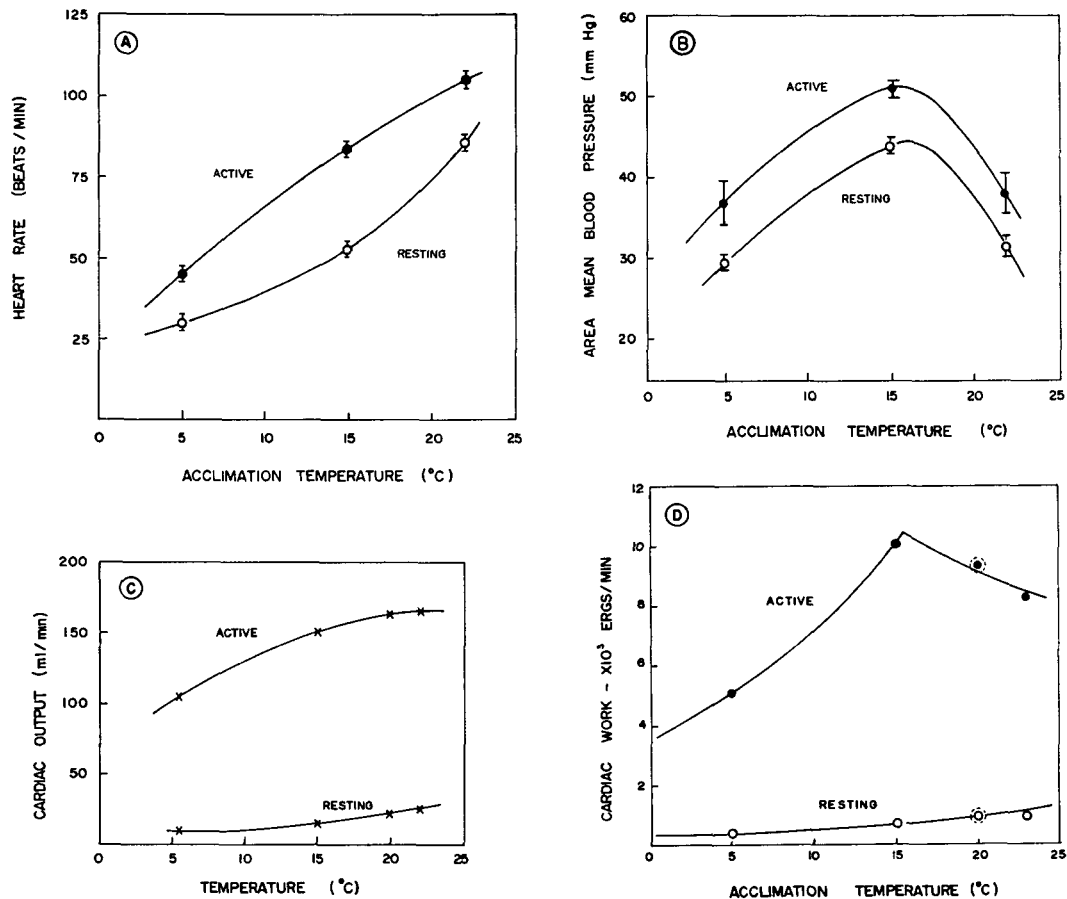


FIG. 4. Heart rate (A), blood pressure (B), cardiac output (C), and cardiac work (flow \times pressure) (D) in relation to acclimation temperature. The circled points in D at 20°C have been

derived from the observed values in C multiplied by the interpolated values in B. (Adapted from Davis, 1968).

creases as the square of velocity, the points plotted as percent of maximum performance do not rise as steeply as the corresponding power requirements would. This accounts for the difference of flatter slope. The decline in metabolic scope above 15°C is thought to be related to limiting oxygen availability (Brett, 1964). Cardiac scope may be responding to the same phenomenon. Whatever the reason, these essential capacities fall off above 15°C. The debilitating effect of high temperatures is multiple.

Three type responses are illustrated in Fig. 5D, with their slopes and terminal points labelled according to Fry's (1947) interpretation of environmental factors. It

is possible to superimpose a general "zone of efficiency" within the thermal tolerance range, based on the depressing effect of low temperatures (below 4°C), the limiting and inhibiting effects at high temperatures (above 18°C), and the span of efficient food conversion (greater than 20% from 5°C to 17°C).

Returning to Table 1, the responses have been totalled according to type. The majority (56%) show a downward deflection, above an optimum temperature. Within this type, 79% of the cases display an optimum at about 15°C. The prediction from such powerful physiological statistics would be that young sockeye would fre-

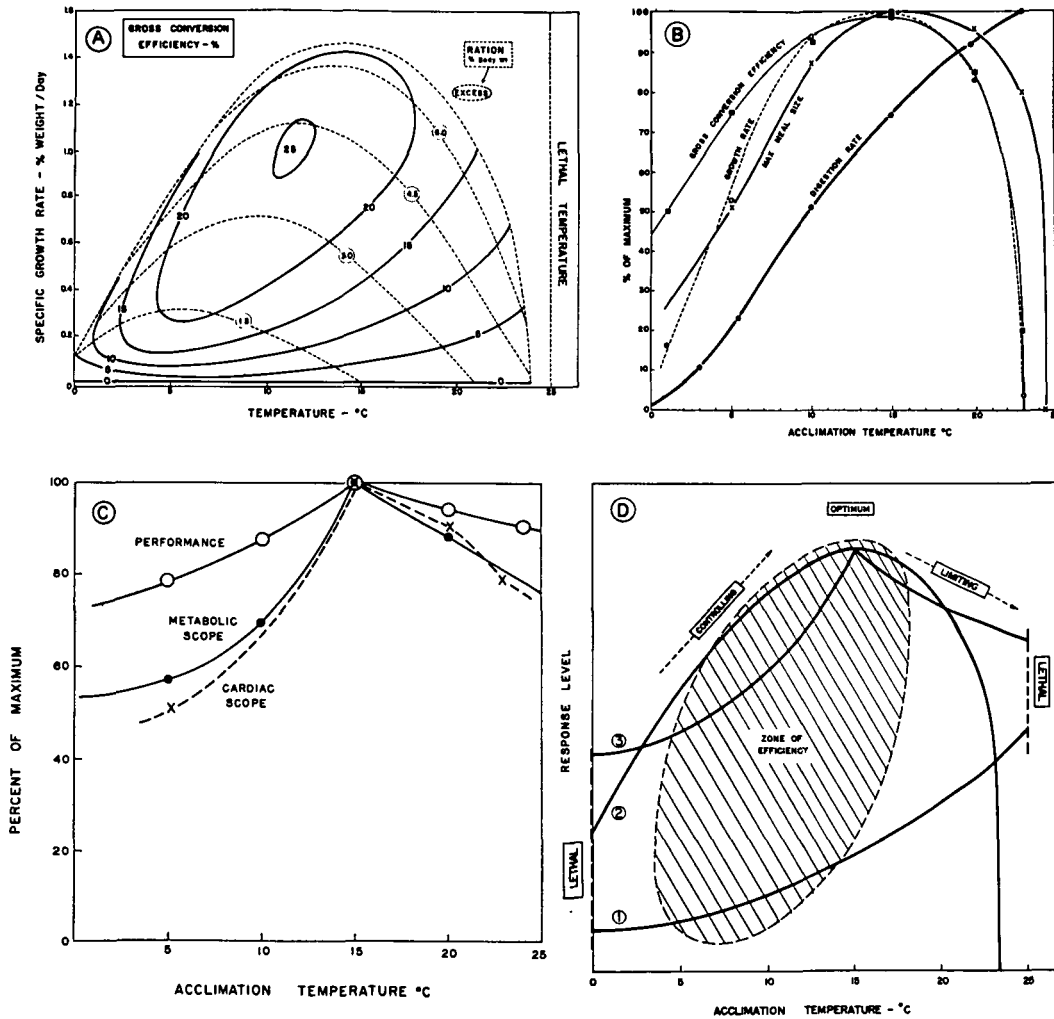


FIG. 5. Food conversion efficiency (A), inter-related systems (B and C), and type responses (D) in relation to acclimation temperature.

quent this thermal region of a lake at such time as seasonal temperature rose to this level and above. The only physiological exceptions to the 15°C optimum occur where ration is restricted, resulting in a downward displacement of the optimum, and some indication of better appetite at temperatures a degree or two above the general optimum.

ECOLOGICAL DESCRIPTION

Early Findings

The genus *Oncorhynchus*, the Pacific

salmon, has evolved a number of divergent ecological patterns within the major behavioral pattern of migrating to sea at an early stage and returning as an adult to spawn in freshwater streams. Upon emerging from the gravel as fry, two of the five North American species (*O. keta* and *O. gorbuscha*) migrate immediately to sea, two species (*O. kisutch* and *O. tshawytscha*) remain for six months or more as stream dwellers, and one species (*O. nerka*) spends one to two years in the offshore waters of lakes. All are plankton-eating in their early life, two (*O. gorbuscha* and *O. nerka*) remain marine

plankton feeders while the other three become fish-eating.

It is the lake-dwelling, plankton-feeding, schooling sockeye that has been the object of greatest study—the most economically valuable of the five salmons, and a highly vulnerable species which unfortunately is declining in abundance throughout its full range (Extensively reviewed by Foerster, 1968). On the average only 6 to 8% of any one year-class survives lake residence to head seaward, usually as 4-6 gram smolts in early spring. By contrast with the ease of procurement when moving downstream as fry or smolt, the difficulties surrounding capture in the vast lake expanse defied success until 1955 when rapidly towed, mid-water trawls were first employed (Johnson, 1956, 1958).

Knowledge of the lacustrine habits was, however, far from lacking prior to that date. There is something to be said for knowing where and when fish *cannot* be found. Also, sockeye predators could be caught. On occasion fresh young sockeye were discovered in the stomachs, which in turn were examined for *their* stomach contents. By combining knowledge of zooplankton abundance and distribution, penetrating speculation on the niche relations of sockeye was possible (Foerster, 1936, 1968; Ricker, 1937). It appeared that as the lake became thermally stratified the sockeye under-yearlings congregated in the vicinity of the thermocline where zooplankton abundance provided ease of capture and where cool subsurface waters were available. Both at dusk and at dawn extensive surface-dimpling revealed a foraging pattern which could not be ascribed to any other species of young fish. Further, the termination of smolt emigration from the lake in spring was highly correlated with the development of a stable thermocline which Foerster (1937) considered blocked further exodus by creating a thermal "blanket."

With the development of the tow-netting procedure, samples of young fish could be obtained throughout the summer, permitting detailed studies on density and distribution (Johnson, 1958, 1961). This

led to confirmatory support for the earlier indirect findings, adding further belief that the mass of young fish remained near the surface (above 5 m) in company with their preferred zooplankton food. Mid-summer surface temperatures were usually about 15° to 17°C in Babine Lake (British Columbia), the scene of most intensive study.

In the light of the physiological evidence on similar optimum temperatures for the majority of basic responses, the strength of the temperature correlation could be ascribed a cause-and-effect relation with rather more than slight justification. At this point of arrival it might well have been considered a closed book—considerable physiological evidence supporting extensive ecological findings.

Recent Discoveries

Despite the wealth of seasonal information, both McDonald (1969, 1971) and Narver (1970) pointed out that even Johnson's advances did not provide direct evidence for other than the periods of day when tow-netting was successful, mostly in late evening and sometimes at dawn. The advent of high-frequency echo sounders and the introduction of deep seine nets (to 16 m) with the support of faster tow-netting allowed around-the-clock sampling. The pooled observations and limnological records revealed an extensive diurnal vertical migration. On a typical day in late August in Babine Lake, young sockeye remain during daylight hours at depth (30 to 45 m) in the cold hypolimnion, rising rapidly at dusk through the thermocline to feed actively near and at the surface. By midnight the majority descend to the upper stratum of the thermocline (10 to 12 m) rising slowly with dawn to feed again, followed by a rapid descent between the hours of 6 and 8 AM to depth. As a result, their daily temperature pattern follows a curve oscillating between 5° and 17°C (Fig. 6). This dynamic state involving voluntary temperature changes of up to 12 Centigrade degrees, with nearly 60% of each day at temperatures between 4°

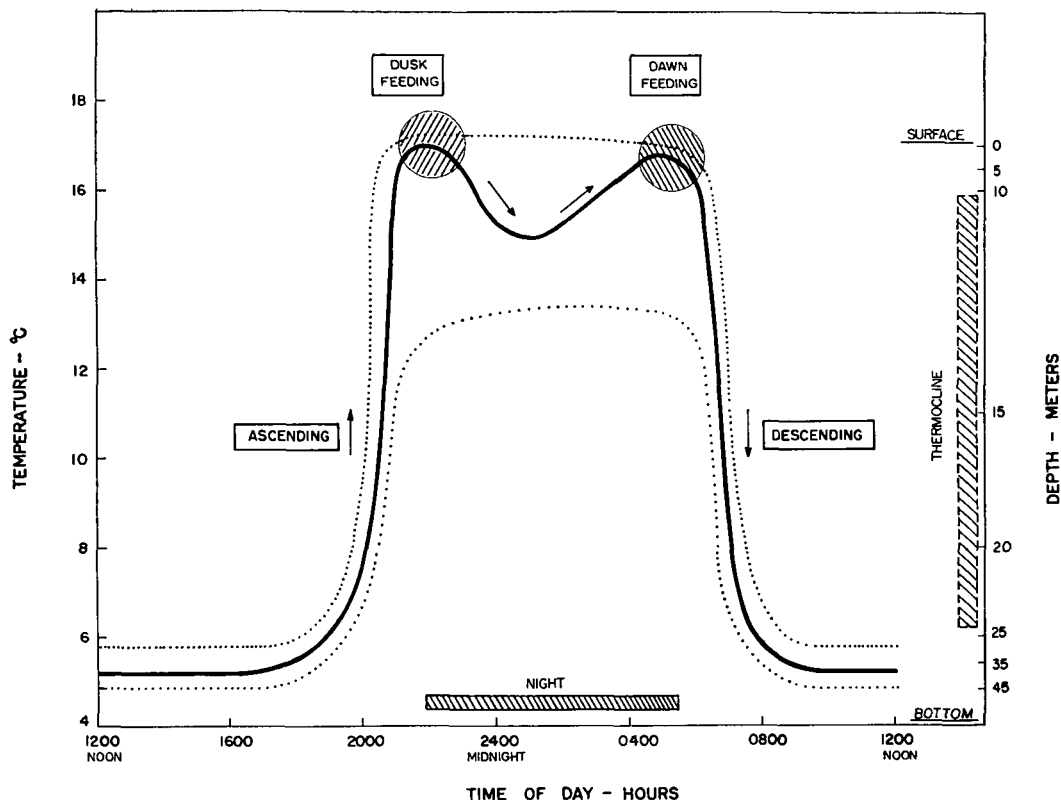


FIG. 6. Pattern of diurnal vertical migration of sockeye in mid-summer with corresponding temperatures. Feeding near the surface occurs over a one- and 6°C, obviously destroys any hypothesis accounting for lake distribution based on single, experimentally-determined preferred and/or optimum temperatures.

ALTERNATIVE HYPOTHESIS

Since the *prima facie* examination of temperature relations does not lead to any ready explanation of the observed diurnal migration, it is necessary either to seek a totally new basis, or to re-examine the temperature responses for some more subtle interrelation of an adaptive nature.

What hypothesis can be postulated to explain the vertical migration of sockeye? Currently there are a number in vogue, namely:

(1) *Unfavorable epilimnial temperatures.* This has already been discussed in part. Relatively high temperatures (above 20°C) are debilitating. Narver (1970)

to two-hour period at dusk and dawn. Dotted lines indicate the general limits of thermal experience. (Adapted from McDonald, 1971).

noted that in warm Lake Washington, sockeye rarely ascend above a depth of 15 m. Avoidance of surface waters was considered characteristic of lakes in the southern range of the species where summer epilimnion temperatures frequently rise above 20°C.

Such an hypothesis may be dismissed for lakes like Babine which rarely get above 18°C. Further, daily retreat to great depth and low temperatures is not accounted for, which, from preferred temperature responses (Fig. 1), would be avoided to the same extent as high temperatures.

(2) *Light (and predator) avoidance.* There is an obvious, strong, temporal correlation with light in the vertical movements, such that exposure to bright light is avoided (Narver, 1970). The dusk and dawn feeding pattern is reminiscent of crepuscular animals which appear to escape

predation by coming out to feed in the twilight periods. Support for this hypothesis is lacking since the predator population is surprisingly scant in Babine Lake despite the predominant abundance of young sockeye (Narver, 1970). In general, it is harder to formulate an acceptable adaptation hypothesis governing numbers of animals on predator-dependent behavior patterns over prey-dependent relations. Abundant prey are more likely to govern predator behavior than vice versa.

But more important in this case, the vertical movement becomes clearly established *only* as the thermal stratification develops, disappearing at the time of the fall turnover. Although light may act as a cue or timing device it does not offer a satisfactory causal explanation.

(3) *Response to prey.* Zooplankton are noted for their diel vertical migrations. Narver (1970) gave this aspect particular attention in Babine Lake. While most zooplankters are concentrated near the surface, of the eight major species only two (*Heterocope septentrionalis* and *Bosmina coregoni*) display vertical movement, and these are in opposite directions. The species (*H. septentrionalis*) that does correspond with the sockeye migration is not dominant in the stomachs at feeding time, but appears in greater relative abundance for samples caught at depth during the day. *Heterocope* is a large and consequently vulnerable zooplankton. The fact that it is one of the lesser components of the diet tends to dispel selective prey response as the basis for the fish behavior. Remaining near the surface during the day, as Johnson (1961) believed, would maintain closer relation with the predominant zooplankton biomass. Since the availability or concentration rather than the average abundance of the prey is important in the energy balance of capture and reward, it is necessary to have far more information on zooplankton behavior before final assessment of this hypothesis is possible. The evidence from *average* zooplankton abundance does not support it.

(4) *Bioenergetic hypothesis.* Following the experimental work on sockeye growth

and metabolism in relation to temperature and ration (Brett, *et al.*, 1969; Brett, 1970a) it appeared quite possible that the diel pattern could be related to most efficient conversion of the available food into growth, a behavior based on energy conservation. High food conversion efficiency is maintained between 5° and 17°C (Fig. 5D); also, maintenance metabolism is reduced by at least one-half going from 17° to 5°C. McLaren (1963) formulated such an hypothesis to account for vertical migrations of zooplankton, suggesting that growth conversion efficiency would be improved in thermally stratified waters by feeding near the surface and digesting in deeper colder water. If temperature *is* involved, the records of significance in Table 1 would have to be drawn more from the exception than the rule—from growth relations under restricted rations (Fig. 3B).

Since the hypothesis stands or falls on the basis of food-limiting conditions, it is necessary to formulate the case by critical examination of a number of pieces of evidence.

BIOENERGETIC HYPOTHESIS

In a study of avian bioenergetics, Zimmerman (1965) expressed the essence of the biological argument thus: "The success of a species is measured by its survival, and to survive is to work, to expend energy. Since economical utilization of energy is intimately associated with adaptation to a particular environment, the bioenergetics of a species is a basic determinant of its niche requirements. . . . It has been demonstrated that the maintenance of a satisfactory energy balance is reflected in the distribution of species, in the adjustment to the annual march of temperature and photoperiod, and in the dispartite range of migratory species. Furthermore, availability of sufficient energy for the young has been suggested as the ultimate factor in the evolution of specific breeding seasons"—to which could undoubtedly be added, specific breeding *areas*.

Assessment of the essential energy relations for sockeye is possible from the vari-

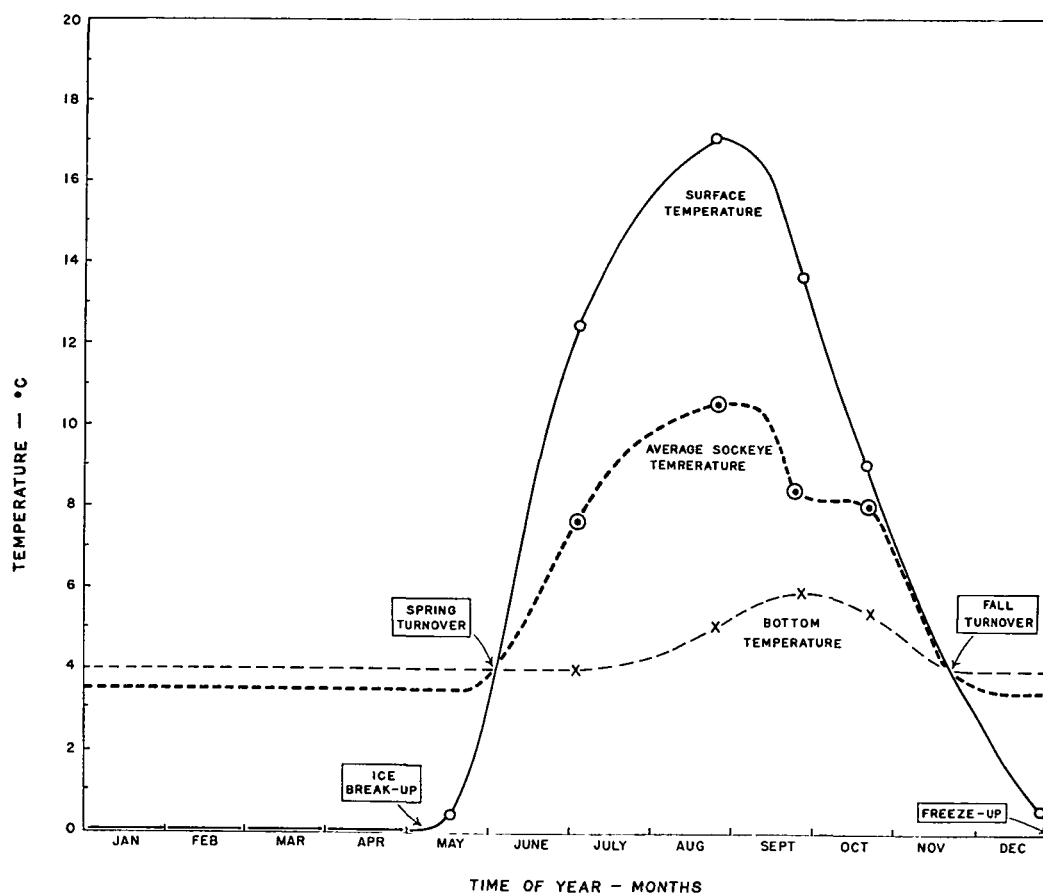


FIG. 7. Surface and bottom seasonal temperatures in Babine Lake, 1967 (Data from McDonald, 1971). "Average sockeye temperature" was com-

puted as daily averages of the temperatures experienced during vertical migration. ous sources dealing with growth and metabolic rate in relation to size, temperature, and feeding intensity (Table 1). Sufficiently accurate estimates can be derived for determining both the extent to which food is a limiting factor in Babine Lake, and the metabolic rates associated with the daily pattern of feeding.

Basic data and Derivations

(1) Temperature history

From the Babine Lake limnological studies and records of sockeye vertical distribution, the annual cycle of temperatures at the surface, near the bottom, and the average experienced by sockeye¹ has been

¹ Computed as daily averages, proportioned by hours according to the temperature at depth—as in Fig. 6 for August.

puted as daily averages of the temperatures experienced during vertical migration.

plotted in Figure 7 (Data from McDonald, 1971). It may be noted that for about 35% of the year the lake is ice-covered; for some 50% of the time it is at 4°C or below; and the surface has an average high temperature of about 17°C in late August.

(2) Observed growth rate

In the years 1966 and 1967, McDonald (1971) recorded the weight of young fish sampled as fry (about 0.2 g) entering the lake early in June from spawning streams, foraging as small fingerlings during the summer and fall (about 3.5 g by Oct. 15), and then as migrating smolts (about 5 g) leaving the lake shortly after ice break-up and spring turnover in May. These are plotted in Figure 8.

(3) Possible growth rate

Two calculations of interest can be

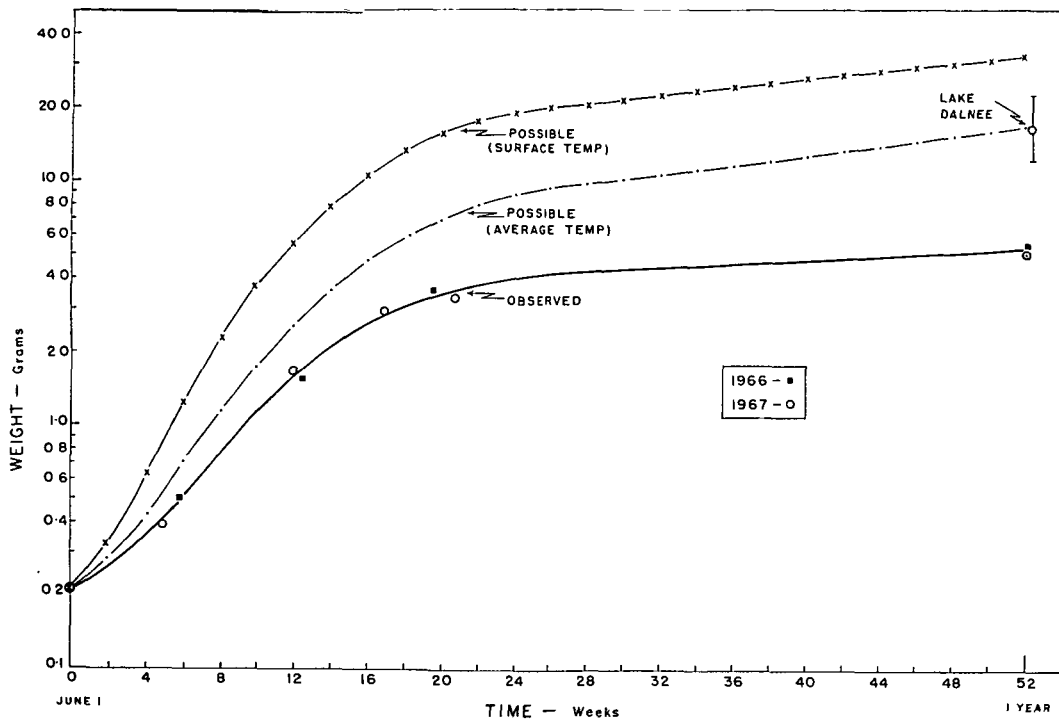


FIG. 8. Observed growth rate of sockeye in Babine Lake (From McDonald, 1971). Possible growth rates computed for satiation ration at "average sockeye" temperatures and for surface tem-

peratures. The mean weight and range of one-year-old sockeye smolts from Lake Dalnee, Kamchatka, is included for comparison.

made of the growth which might have been achieved if ration were not limiting, first, at the average temperature experienced, and second, that which could be attained at the maximum annual temperature cycle. The second obviously implies no diel vertical movements, providing an "ultimate" course available to the fish.

The experimental data on growth rate \times size \times temperature \times full ration were programmed on matrix tables and computed to provide the weight estimates plotted in Figure 8. By the middle of October the *observed* weight was approximately 3.5 g, the *possible* (average temperature) was 7.2 g, and the *ultimate* (surface temperature) was 15.8 g. It is apparent that observed weights were from 105% to 350% less than the computed possible weights. Because gross food-conversion efficiency would likely decrease with increasing size, the doubling of weight would require more than twice the food intake. This adds further

confirmation for, and extends, the suspected food-limited state which was concluded by Johnson (1961) from a study of food-abundance and density-dependent relations in various basins of the lake. It is of interest that the weight of the smolts which could be expected from computations on possible size for *average temperature* was almost exactly the same as the mean size of the one-year-old sockeye smolts (16.5 g) which emigrate from highly productive Lake Dalnee, Kamchatka (Fig. 8) (Krogius and Krokhin, 1948; Table 65 in Foerster, 1968). This lake is in a fairly cold climatic zone, where lakes freeze over for a number of months, not unlike Babine Lake.

It can be concluded that the major hinge of the energetic hypothesis is supported—energy intake is decidedly sub-maximal.

(4) Feeding and digestion rates

The fact that intake is below the pos-

sible level does not actually mean that food mass is limiting, but rather that food is not taken to the point of daily satiation (full ration). An immense biomass of zooplankton (above the thermocline) is obviously still present at any one time. The density-dependent observations of Johnson (1961), however, strongly suggest that the availability is sufficiently reduced to make the reward of further cropping an inefficient energy investment.

There remains the obvious question that if the energy dissipated by expensive maintenance metabolism at high temperatures can be saved at low temperatures why do the fish not retreat to depth during the dark hours of night when prey visibility is a serious handicap to further feeding? A vertical distance of 40 m only represents about 5 minutes swimming (for a 5 cm fish at 3 L/sec). This nocturnal behavior appears to support the thesis of predator avoidance by cover of darkness.

The energetic analysis derives from studies of voluntary food intake, rate of digestion, and return of appetite which are each distinctively temperature-dependent (Brett, 1971; Brett and Higgs, 1970). At a single feeding the stomach of small fish can hold about one-half the amount which can be consumed in a day on multiple feedings at 15°C. Governed by rate of digestion, the appetite of satiated² fish builds up rapidly following a 6 to 8 hr digestive pause. At 6°C the equivalent pause would be of the order of 20 to 30 hrs. Consequently, descent below the thermocline would delay the processing of the heavier, dusk feeding blocking the refeeding opportunity which is apparently presented at dawn. A compromise is therefore imposed in the interest of increased daily energy intake.

BEHAVIORAL THERMOREGULATION

The validity of the bioenergetic hypothesis remains to be tested, a task which is currently underway. Whatever the out-

² The fish in nature are likely not satiated. If potential stomach volume is below the maximum, appetite will return proportionately faster (Tyler, 1970).

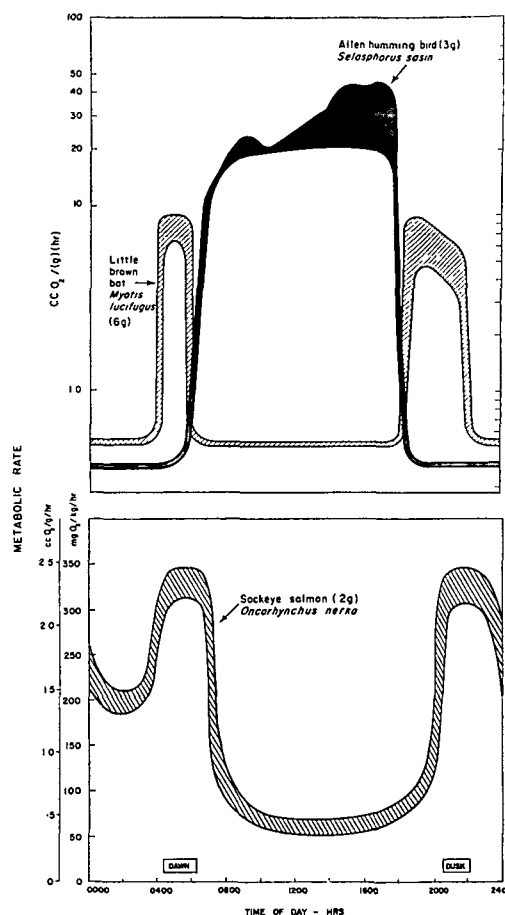


FIG. 9. Schematic representation of daily mid-summer metabolic rates of sockeye compared with similar compilations for the Little brown bat and the Allen humming bird (The latter two taken from Gordon, 1968).

come, and whatever the final resolution, the behavioral phenomenon inducing daily oscillations in body temperature must induce a corresponding oscillation in metabolic rate, coupled with the phased metabolic demands imposed by periodic feeding and digesting. It is possible to compute the likely pattern, using preliminary data from experiments on metabolic rates accompanying various feeding levels and temperatures (Brett, 1970a). This schematic presentation is compared (Fig. 9) with similar compilations for the Little brown bat and Allen humming-bird, both of which undergo daily torpor periods, apparently to conserve energy (From Gordon

1968). The metabolic resemblance is striking. If the foregoing hypothesis is correct, the conclusion is inescapable that sockeye have evolved a pattern of thermoregulation peculiarly adapted to maximizing growth, through the selective pressure of bioenergetic efficiency. Whereas certain endotherms have had to compromise the daily costs of complete homeothermy with heterothermic periods, a comparable form of metabolic pacing has apparently evolved in this aquatic ectotherm, an ectotherm which is denied the direct radiant source of heat so effectively exploited by reptiles but has, instead, utilized the available means of heat flow.

CONCLUDING COMMENT

It might well be wondered what is the significance of the predominantly optimum temperature of 15°C derived from the physiological studies. This remains a very meaningful parameter for all cases such as performance, metabolic scope, and cardiac function and will apply with as much physiological significance in the natural environment as in the laboratory. Sustained performance can confidently be expected to be maximum in the vicinity of 15°C no matter where the animal is. The field condition which dictates so much of the energetic physiology of young sockeye is *restricted ration*. Relatively few experiments have been performed where this biotic factor has been coupled with an abiotic variable such as temperature (or light, or salinity etc.). Consequently, from the compilation in Table 1, it turned out that it was necessary to go to the exceptional case rather than the general case. It was the *shunt* in optimum temperature for growth to successively lower levels, as ration was progressively limited, which provided the laboratory insight for a possible explanation of a field condition. Further it is the retention of a high food conversion efficiency over the full range of the daily temperatures experienced which becomes most meaningful.

Finally, it must be admitted, it is inherently difficult to examine existing condi-

tions and deduce the important biological factors which have occurred in the past to explain the present. While a major force in evolving the diurnal pattern can be attributed to energetics, both the prey of sockeye and the predators of sockeye are in a dynamic state of balance with *their* total environment. The present state of the sockeye population is a product of a complex interaction of all the abiotic and biotic factors.

Mauchline and Fisher (1969) have reviewed information on the diurnal movements of euphausiids and concluded that vertical migration probably confers a number of benefits on the organisms.

It would be hard to argue that the physiologically possible "energy bonus" from vertical migration was not a very meaningful segment in the overall benefit conferred.

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