SOME EFFECTS OF ACCLIMATION, ACUTE TEMPERATURE EXPERIENCE, AND SIZE, ON THE SUSTAINED SWIMMING SPEED OF JUVENILE COHO SALMON (ONCORHYNCHUS KISUTCH).

by

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ABSTRACT

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Swimming speeds of coho salmon juveniles have been investigated with respect to acclimation temperature and acute (test) temperature experience. Sustained swimming speeds were approximated in terms of critical swimming speeds; the latter is related to the time to fatigue in samples of fish exposed to incremental increases in water velocity in an experimental water tunnel. Three series of tests were conducted between September, 1968 and May, 1969 on coho ranging between approximately 7½ and 9½ cm. total length.

Regression relations between critical velocities and acclimation and test temperatures were developed by response surface analysis using a non-linear second degree polynomial as a model.

Maximum performance (5.8 lengths/second) occurred at acclimation and test temperatures near 20° C. At lower acclimation temperatures, maximal performance was found at temperatures greater than those of acclimation, defining a ridge of near-maximal performance. Thus, maximal performance over a range of test temperatures is not necessarily found at a test temperature equal to that of acclimation. In addition, maximum performance over a range of acclimation temperatures is not necessarily found at an acclimation temperature equal to that of testing. This lack of correspondence over the performance surface changes progressively, attenuating at acclimation and test temperatures in the vicinity of 20° C.

Seasonal differences in performance were observed, although not clearly defined. These involved a change in the shape of the performance surface. In addition, a dependence of swimming performance on size was recognized, although the relation could not be defined quantitatively.

Comparison of performance of the coho with that of the sockeye salmon juveniles suggested that the former may be better equipped to perform in warm environments.

A hypothesis is advanced suggesting that a relation, in terms of temperature, may exist between the performance optimum, those for metabolic scope and growth on excess rations, and for the final temperature preferendum.

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INTRODUCTION

Temperature is probably the most potent physical factor in the aquatic medium. This is especially true for fishes, which are obligate poikilotherms throughout their life. The high specific heat of water, combined with rapid circulatory exchange through the gills, makes maintenance of an independent body temperature impractical. While the elevation of body-muscle temperature has been noted in tuna (Barrett and Hester, 1964) it may be stated that fishes are generally thermal conformers, as they appear to expend no energy to maintain a constant body temperature. Thus, all the activities of fishes are, in varying degrees, subject to temperature. Brett (MS) suggests that for fishes temperature may be considered as the "master ecological factor" of the aquatic environment.

The subject of this study, the coho (Oncorhynchus kisutch, Walbaum), is an anadromous salmonid that characteristically spends its first year in fresh water, although the period of fresh water residence may vary. The coho is common in small streams and along the shorelines of lakes. Temperatures in these areas may become quite high (20°C +) and may be subject to considerable fluctuation.

Two other species of Pacific salmon, the chinook (O. tshawytscha, Walbaum) and the sockeye (O. nerka, Walbaum) also spend up to a year or more in fresh water. Characteristically these species inhabit large streams and deep lakes respectively, where more uniform, lower temperatures prevail.

While these species are taxonomically closely related, their distinctly different habitats suggest that they may display differences in their response to temperature. The coho would be expected to be the most eurythermal of these salmonids, owing to its relatively warm and unstable habitat.

Attempts to assess the effects of temperature on a species are often extremely difficult under field conditions. The environment consists of a complex of biotic and abiotic factors which may act independently or in concert, and the fish responds not to individual factors, but to the complete environment. To interpret adequately the effects of temperature in the unconstrained environment, the ecologist requires information on the effects of this factor alone and in combination with other factors of importance. Data of this type are best obtained from controlled laboratory studies.

The first step in a laboratory study of the effects of temperature on a species is to determine the temperature tolerance. As described by Fry (1947), temperature tolerance is dependent upon thermal history, or the acclimation temperature. When both upper and lower tolerance levels are considered, a zone of temperature tolerance may be described. The area enclosed by the tolerance zone, or tolerance polygon, has been measured in terms of acclimation and test temperatures to provide a quantitative estimate of the eurythermicity of the species, expressed as "degrees centigrade squared."

Brett (1952) determined the tolerance zones for the five species of Pacific salmon. While the size of their tolerance zones shows some correlation with their respective habitats, the ability of all five species to exceed normally encountered extremes suggests that temperature tolerance per se plays a relatively minor role in limiting their distribution.

To further assess the role of temperature in the ecology of Pacific salmon, more subtle measures of viability are required. Brett (1956, 1958) suggested that the ability of a species to be active within its tolerance domain may be of more importance in determining the success of a species than the actual dimensions of the tolerance domain. He suggested the presence of smaller domains within the temperature tolerance zone, defining boundaries for effective growth, activity and reproduction.

Within each of these smaller domains, the response in question may be optimized under certain conditions of acclimation and test temperatures. If these responses can be assumed to provide estimates of the physiological well-being of the species, its distribution according to temperature may be dependent upon both the dimensions (shape) of these response domains and the position of their response optima.

The present study describes a laboratory investigation of the effects of acclimation and acute temperature experience, and to some extent the effect of size, on the sustained swimming speed of juvenile coho salmon. The term "acute temperature experience" is used to denote the testing of fish at temperatures other than those of acclimation.

Sustained swimming speeds measure active capacity of the integrated organism, in contrast with capacity measurements of individual systems or organs within the animal. Swimming speeds indicate the energy available to the fish after maintenance requirements have been met. Active capacity is dependent upon the difference between standard and active metabolism (metabolic scope). However, for a given change in temperature, swimming speed changes are much less than those for metabolic scope. In general, metabolic scope rises geometrically with increased swimming speed (Fry, 1967). As swimming speeds are direct measures of active capacity, they may be readily translated in terms of the organism's ability to maintain position in a current, obtain food, or defend a territory. Also, active capacity and growth optima may coincide (Fry, 1964). Hence, the measurement of sustained swimming speeds may provide one biologically valid estimate of the coho's physiological potential under varying temperature conditions.

The ability of the juvenile coho to inhabit warm and relatively unstable environments may be related to the dimensions of its temperature performance domain and the position of its performance optimum within this domain. A number of biologically important responses to a given factor or combination of factors may define physiological optima for a species (Alderdice, MS). The present study investigates one response to test and acclimation temperatures; it is intended to provide a step toward improved knowledge of physiological optima for *O. kisutch*.

MATERIALS AND METHODS

Experimental Fish

Source and culture.

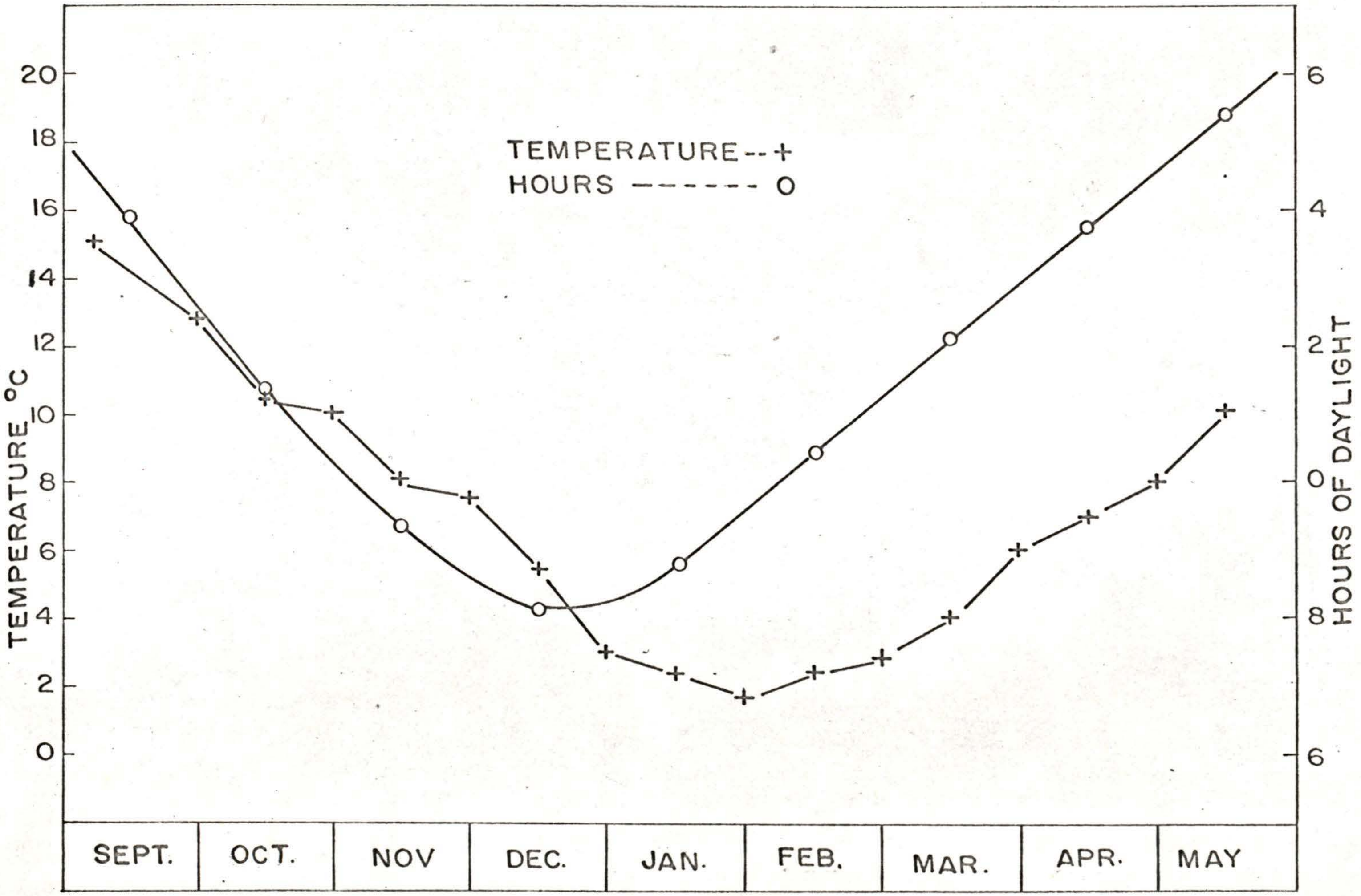
Exercise prior to testing may significantly affect the swimming ability of fish (Brett et al., 1958; Brett, 1965). Assuming that individuals from a wild population would be better exercised than cultured stock, it would have been desirable to obtain wild specimens and test them as soon as thermal acclimation was complete. However, the difficulty in obtaining adequate numbers of wild coho during the winter months made this approach impractical.

An alternate procedure was adopted. Wild coho fry were collected with hand seines from Kinkade Creek, a tributary of the Little Qualicum River, Vancouver Island, B.C. The fish were transferred to holding facilities at the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C. and held there during the experimental period, from September, 1968 to May, 1969. An initial stock of 500 coho was collected on July 22 and 23, 1968. These fish were used for trial runs during August, 1968 to establish a satisfactory test procedure. An experimental stock of 2500 fish was then collected during the period August 28 to September 5, 1968. These fish were approximately 5½ months old and their mean total length was about 6 cm. (size range approximately 4 to 8 cm).

After collection, the fish were held in a large circular tank (3' x 8') located outdoors and provided with a partial cover. The fish were subject to natural photoperiod, and seasonal and diurnal temperature fluctuations (Fig. 1). A continuous inflow of fresh water to the tank produced a moderate current against which the fish swam. The level of activity was quite low, probably not in excess of one body length per second. Commercially prepared, pelleted food (Abernathay formula, Salmon-Cultural Laboratory, Longview, Washington) was used. This diet was supplemented with frozen brine shrimp (Artemia) for the first few months.

Figure 1

Variation in photoperiod (civil) and ambient
water temperatures during the experimental period
(September 1968 - May 1969).


TEMPERATURE --+
HOURS ------ O
TEMPERATURE °C
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18
16
14
12
10
8
6
4
2
0
HOURS OF DAYLIGHT
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4
2
0
8
6
SEPT.
OCT.
NOV
DEC.
JAN.
FEB.
MAR.
APR.
MAY

While the experimental stock could not be classed as "wild", the work of Vincent (1960) on domestication of brook trout suggests that the experimental stock would retain much of the stamina of wild fish. The low mortality and absence of disease observed suggests that the fish remained in good condition throughout the experimental period.

A sample of 10 fish was used in each swimming speed test, and it was necessary to re-use some fish during later tests. To allow adequate time for recovery from testing and acclimation to stock tank temperatures, used fish were held for a minimum of one month in a smaller circular tank (3' x 3') located beside the stock tank. After the holding period, the used fish were transferred back into the experimental stock.

Acclimation of test fish.

Groups of approximately 100 fish were removed from the stock tank for thermal acclimation prior to testing. Any obviously weak or injured fish were discarded during selection for acclimation. The data of Brett (1965) and Bainbridge (1958) indicate that size affects performance. Therefore, fish to be acclimated were selected according to size. Fish were anaesthetised (1:10,000 MS 222 for 2 to 4 minutes) and selected for a given total length ±0.25 cm. Two advantages were gained by this procedure. First, by beginning a replicate with fish slightly larger than the mean size of the experimental stock, it was possible to maintain this size for each acclimation group, in spite of continuing growth of the fish during the time required to complete one replicate of the experimental design. Second, it was found during preliminary tests that aggressive behavior was displayed during swimming tests, even at swimming speeds near fatigue levels. This may have caused premature failure of some fish. Uniform size selection appeared to reduce the level of aggression.

Groups of test fish were acclimated in oval, 100-litre fibreglass culture tanks (Alderdice et al., 1966) located in the laboratory. Fresh water at three temperatures was available for each tank: ambient temperature (Fig. 1); heated (26°C); and refrigerated (3°C to 5°C). By appropriate mixing, it was possible to produce an inflow to the tanks at a temperature approximately 1°C below the desired acclimation temperature. Balancing this inflow against a thermostatically controlled heater allowed control of temperature within ±0.1°C.

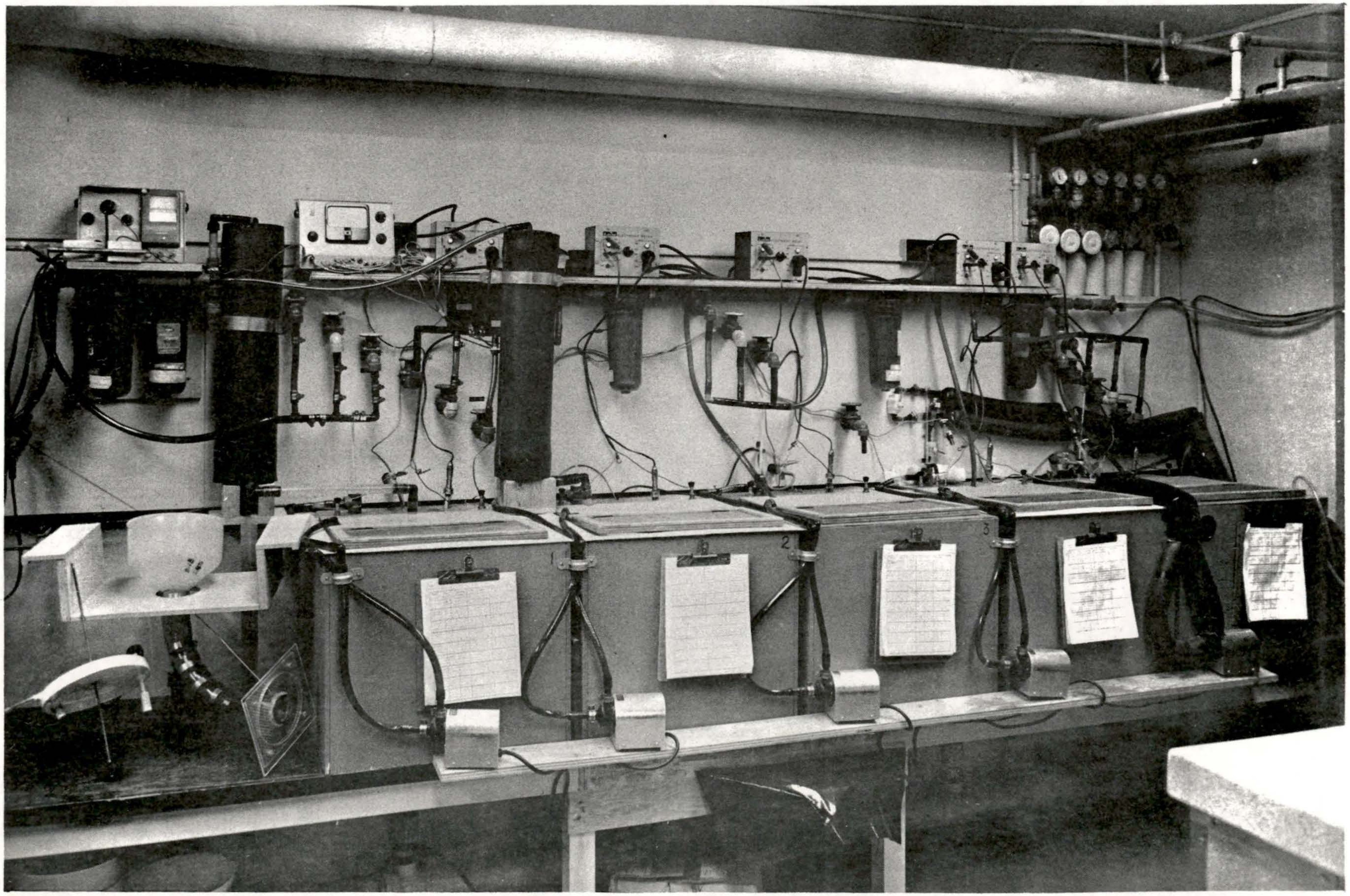
Five acclimation tanks were available (Fig. 2). Two of these were equipped for high temperature acclimation by the addition of gas-stripping columns to remove excess oxygen and nitrogen from the inflowing water. Two tanks were modified for low temperature acclimation by the addition of stainless steel cooling coils. Insulation of one of these tanks allowed acclimation temperatures to be held as low as 2°C. A low net inflow of water was required in order to maintain precise temperature control.

Electric pumps were installed on each tank to recirculate water and provide a current. Water velocities varied considerably. Maximum velocities were approximately 15 to 20 cm/second near the pump outlets and minimum velocities of less than 3 cm/second were recorded in some portions of the tanks. The average velocity was about 6 to 8 cm/second, or slightly less than one body length/second.

Two large fluorescent lamps mounted above the acclimation tanks provided lighting. Photoperiod was controlled by a time clock

Figure 2

Photograph of the acclimation tanks. The pumps at the front of the tanks recirculate water to provide a current. The two tanks to the left (1 and 2) are equipped with gas-stripping columns. The two to the right (4 and 5) are equipped with stainless steel cooling coils. The thermoregulators at the rear of each tank and the relays above control stainless steel heaters in each tank. Temperature is continuously recorded by the scanner and strip-chart recorder in the top left of the photo. The entry device (see text and Fig. 6) is also shown to the left of the tanks.



regularly adjusted to provide normal day-length (Fig. 1.; ±30 minutes).

During acclimation, fish were fed daily, using the diet described for the outdoor stock. The fish were not fed for a minimum period of 12 hours prior to testing.

Rates of acclimation to temperature have not been described for salmonids. Rates of gain of heat tolerance for Carassius auratus (Brett, 1946) and acclimation periods used for Pacific salmon (Brett, 1952) provided rough guidelines for establishing minimum acclimation periods in the present study. Minimum periods of 2 to 3 weeks appeared desirable, the time being dependent upon the direction and magnitude of the temperature change required. The actual acclimation times to the beginning of testing for each acclimation group are shown in Table I. Owing to the time required to test each group, some groups were held at acclimation temperature for extended periods prior to use. While Brett (1952) found no differences in temperature tolerance after extended acclimation, the longer periods in this study were undesirable, especially for high temperature acclimations where the risk of disease could be greater (Table I).

Active Capacity Apparatus

Types of apparatus.

Various types of apparatus have been used by previous investigators for the determination of swimming speeds. Fry and Hart (1948b), Bainbridge (1958), Paulik et al. (1957), Brett et al. (1958) and others have used rotating annular troughs. While annular troughs can be used to measure cruising speeds, it is difficult to

Table I. Days of acclimation prior to testing.

Acclimation Temperature (oC)	Initial Temperature (°C)	Minimum Acclimation (Days)
11.0	15.0	14
14.0	15.0	20
8.0	15.0	22
17.0	13.3	18
5.0	8.0	29
2.0	5.0	23
23.0	13.3	21
20.0	13.3	20
17.0	13.3	56
14.0	7.7	17
11.0	7.7	32
8.0	5.5	20
5.0	2.5	16
2.0	2.6	16
23.0	2.6	15
2.0	2.0	10
20.0*	2.6	46
17.0	1.9	44
5.0	3.1	15
14.0	3.2	20
8.0	4.0	16
11.0	4.0	24
20.0	7.5	14
5.0	6.0	19
14.0	6.0	24
23.0	6.0	20

* This group contracted a fungus disease.

force a fish to swim maximally in them. Screens or electrodes may be added to the annular trough to stimulate the fish to swim, but these produce increased slippage between the water and the trough, making actual water velocities difficult to determine. Because of the circular design of such "fish wheels", some velocity differences also occur between the inner and outer edges of the trough.

Straight, open troughs have been employed by Reimers (1956) and Vincent (1960) but it is difficult to obtain precise water velocities in these troughs. "Wall drag" is often considerable, especially in troughs with rectangular cross-sections.

"Closed-circuit" water tunnels have been used by several investigators (Brett, 1964; Blazka et al., 1960; Davis et al., 1963; Smit, 1965; Thomas et al., 1964). These tunnels have the advantage of more precise velocity control, and a reduction of wall drag is possible. Also, fish may be stimulated to perform maximally in this type of apparatus. There are two basic types of recirculating water tunnels, those designed for measurement of metabolic rate as well as swimming performance (swimming respirometers) and those designed for measurement of swimming speeds only (active capacity tunnels).

The overall volume of respirometers must be limited to allow measurement of oxygen consumption, and test chambers are therefore relatively small. This problem was partially solved in a respirometer where the test chamber was of a much larger diameter than the remainder of the tunnel (Brett, 1964). Expansion and contraction cones at each end of the test chamber apparently reduced the undesirable flow patterns which would normally result from an abrupt change in tunnel diameter. A different approach was used by Blazka et al. (1960) in the design of their respirometer. This apparatus consisted of two horizontal concentric cylinders. Water was driven through the inner cylinder by a propellor and returned between the two cylinders. The design necessitated close proximity of the propellor and test chamber, a situation which may have had undesirable effects on the test fish. As respirometers must be sealed to measure oxygen consumption, testing groups of fish is often difficult, as fatigued fish cannot readily be removed.

Tunnels designed for measuring swimming speed only are not subject to size restrictions. Larger test chambers are possible, allowing the fish more freedom of movement. As there is no need to restrict overall water volume, portions of the tunnel leading up to the test chamber may be large in diameter, reducing undesirable flow patterns in the chamber. As the active capacity tunnel does not require sealing from the atmosphere, removal of spent fish is facilitated. This attribute, combined with the tunnel's large size, allows testing of groups of fish in order to amass comparative data.

General construction of the apparatus.

The water tunnel used in this study was built specifically for swimming speed (active capacity) measurements (Figs. 3 and 4). It was designed by the staff of the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C. and fabricated at the Pacific Naval Laboratory, Esquimalt, B.C.

Water was forced through the tunnel (Fig. 3) by a five-blade propellor, belt driven by a 3/8 H.P. constant-speed electric motor. A hydraulic drive unit (not shown) allowed precise control of propellor R.P.M.

Figure 3

Basic construction of the active capacity tunnel.

1. turbulence screens
2. test chamber
3. shocker area
4. rear screen
5. observation ports
6. recovery chamber
7. screen
8. cooling coils
9. heaters
10. propellor
11. propellor shaft
12. drive pulley
13. temperature sensor

The direction of water flow is indicated by the large arrows.

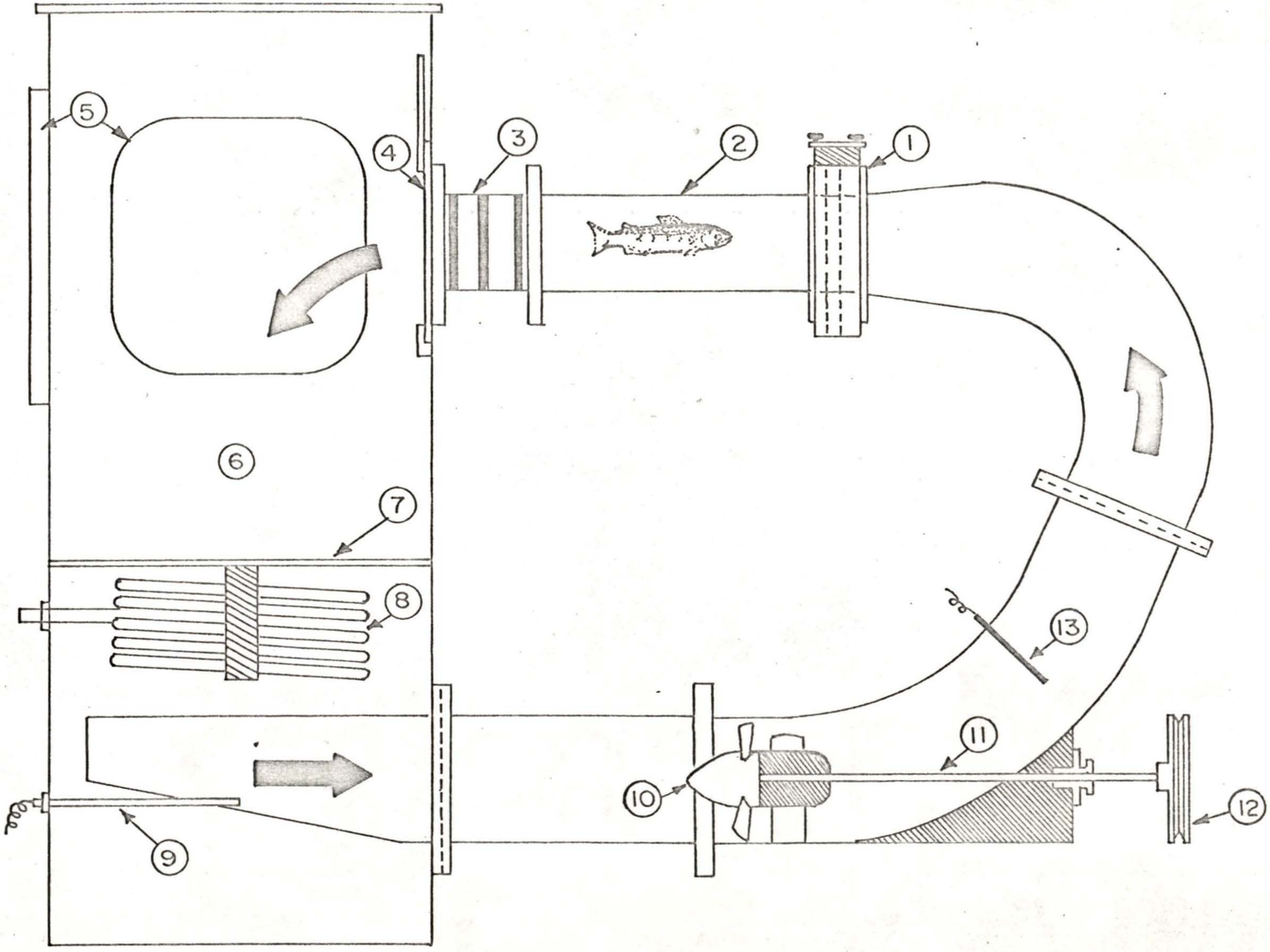

5
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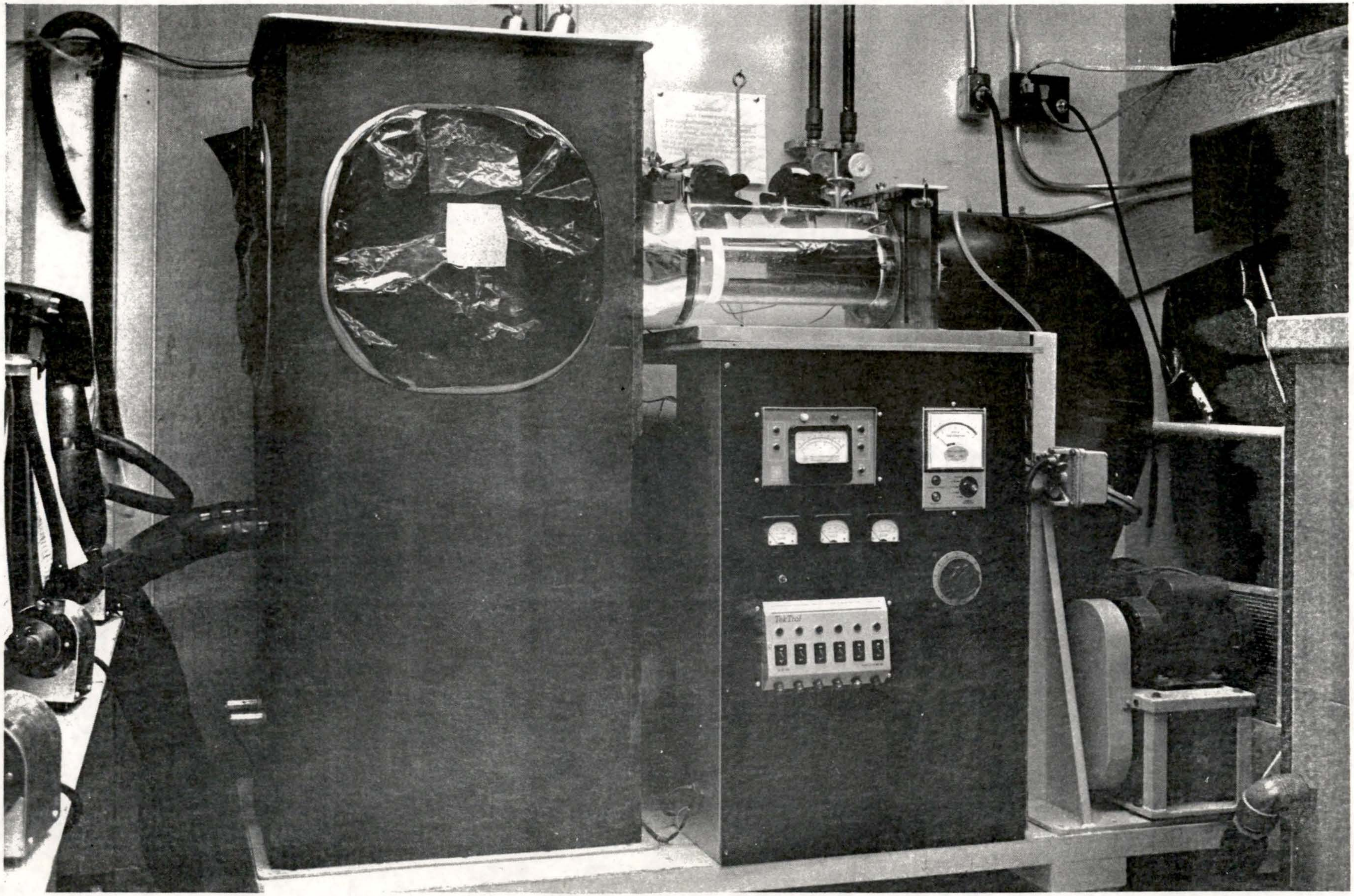
Figure 4

A photograph of the active capacity tunnel. The observation ports (upper left) are partially covered with plastic sheeting. The electric fans and shrouding around the test chamber prevent condensation. The temperature controller, tachometer and shocker voltage controls are mounted in the centre panel. The electric motor and the hydraulic drive unit below are visible in the lower right corner of the photo.



TekTrol

The propellor and the major components of the tunnel, with the exception of the test chamber, were fabricated from fibreglass. Tunnel diameter, with the exception of the test chamber, was 8 inches (inside diameter) and the total volume of the apparatus was about 550 liters.

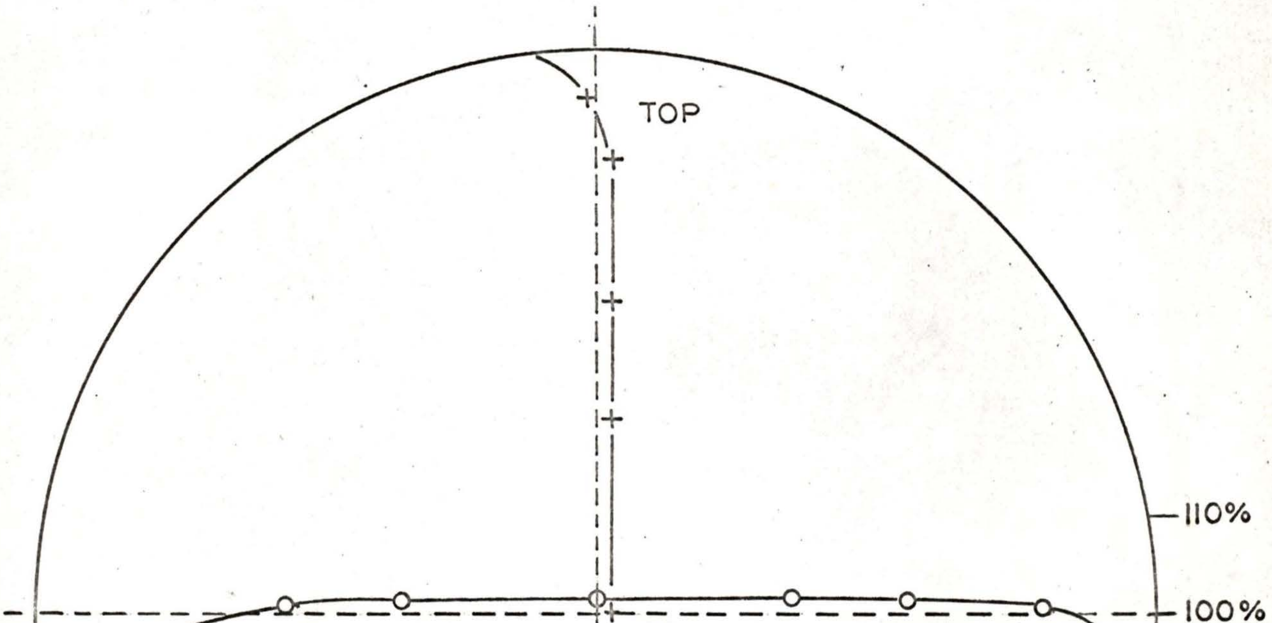
The water temperature in the tunnel was controlled by balancing two 500 watt heaters against a flow of ethylene glycol pumped through cooling coils. A temperature sensor was located between the propellor and the test chamber. A pair of solenoid valves, actuated by the sensor, allowed coolant to circulate through the coils as required. Initial experiments indicated that low test temperatures were difficult to obtain. Therefore, the entire tunnel, with the exception of the test chamber, was insulated with 3/4 inch neoprene rubber sheeting. Double plexiglass windows were constructed for the observation ports to aid insulation and prevent condensation at low temperatures. After insulation of the tunnel, test temperatures could be held within ±0.1°C. or less, although ice formation on the cooling coils was encountered with 2°C. test temperatures at low velocities.

The test chamber.

Two stainless steel screens were inserted at the forward end of the test chamber to reduce the macro-turbulence caused by the propellor and minimize "wall drag" in the test chamber. The screens produced a micro-turbulent flow which resulted in an extremely flat velocity profile in the test chamber (Fig. 5).

Figure 5

The velocity profile in the test chamber. The points shown are percentages of the mean water velocity.



PERCENTAGE OF MEAN VELOCITY

The test chamber was constructed of clear acrylic tubing, 5 3/4 inches I.D. (inside diameter) and 24 inches in length. The turbulence screens formed the forward boundary of the chamber and a removable nylon monofilament screen formed the rear boundary. Several stimuli were used to ensure maximal swimming performance from the fish. Strips of black plastic with transverse white bars were attached to the top and bottom surfaces of the chamber to provide visual orientation points for the fish. A light gradient was established by brightly illuminating the recovery area and the rear of the chamber. The apparatus was located in a darkened room, and a half-silvered mirror in front of the test chamber allowed the operator to observe the fish without being seen. At the rear of the tunnel, three charged graphite rings produced an electric barrier, further inducing the fish to perform maximally. It was initially suspected that the combination of orientation points, light gradient and shocker would provide sufficient stimulus to keep the fish in the test chamber. However at low velocities, aggressive behavior and spontaneous activity often resulted in a fish entering the electric barrier while swimming downstream. There it would receive a shock and dart through into the recovery chamber. The rear screen was added to the test chamber to prevent this.

Calibration.

A calibration curve was constructed relating water velocities in the test chamber to propellor shaft R.P.M. Shaft revolutions were measured by a photoelectric tachometer. Two instruments were used to measure water velocity at the rear of the test chamber. The initial calibration and the cross-sectional profile were determined with a direct-reading Pitot manometer. As the velocity profile (Fig. 5) indicated that the centre line velocity was less than 2% above the mean velocity, the calibration curve was constructed using centre line velocity. An "Ott" current meter was used for subsequent calibrations, as this instrument was more accurate than the Pitot tube.

During the course of the experiments, detritus accumulated on the turbulence screens. This impediment to flow resulted in a reduced velocity for a given propellor speed. The screens were cleaned daily and the calibration was checked each week after the discovery of this fact. The regular cleaning was effective, as the calibration checks showed no significant deviations from the initial calibration.

Test Procedure

Method of testing.

Several measures of swimming speed may be used to determine the active capacity of fish. Cruising speeds, as defined by Fry and Hart (1948b) and Brett et al. (1958) were not suitable for this study; the method requires adjustments of the water velocity to be made which are dependent upon the performance of the individual being tested.

Fixed velocity tests will accurately estimate maximum sustainable speeds, but a series of time consuming tests is needed to establish a fatigue time-velocity curve for each set of experimental conditions.

Critical swimming speeds, as defined by Brett (1964), were chosen as the most suitable method of approximating maximum sustained speeds. These tests could be performed in an 8 to 10 hour period, were suitable for group testing, and have been shown to approximate the results obtained from fixed velocity tests. Critical swimming speeds are determined by a stepwise procedure: the water velocity is incrementally adjusted until the fish fatigue. It has been demonstrated by Brett (1964, 1967) that if velocity increments about 1/8 the maximum sustainable speed are applied for periods of one hour, the fatigue velocity will approximate the true sustainable velocity.

Unless the fish fatigue exactly at the beginning or end of a given velocity increment, the actual velocity causing fatigue must be estimated. The method used (Brett, 1964, 1967) involves adding a fraction of the last imposed velocity increment to the highest velocity maintained for the full hour. The fraction is proportional to the time the fish was able to continue swimming. For example, if a fish was able to sustain a velocity of 35 cm/sec. but fatigued after 30 minutes at 40 cm/sec., the critical swimming speed would be estimated at:
35 cm/sec. + 30/60 x 5 cm/sec. = 37.5 cm/sec.

To determine the magnitude of velocity increments for a given test, a prior estimate of the velocity attainable at each set of test conditions is required. Care must be taken that this estimate does not seriously overestimate the actual performance of the fish. If the imposed velocity increments are too large, the fatigue velocity will overestimate the actual sustainable speed. Brett (1964) suggested that a minimum period of about 5 hours swimming was required for sockeye to reach true sustained swimming speeds. In the present study, the velocity increments used in a given test were determined from pre-test estimates of performance. For example, if the swimming speed under certain test conditions was expected to be about 4 lengths/second, velocity increments of 4/8 = 0.5 lengths/second would be used. Fish averaging 7 cm long would be subjected to water velocities increasing by 7 x 0.5 = 3.5 cm/second each hour and would reach fatigue velocities after about 8 hours of swimming.

Test strategy.

Much of the testing in this study was done under acute temperature experience, that is, test and acclimation temperatures were not equal. It was desirable to maintain acclimation temperatures until the fish had actually entered the test chamber and to allow them some time to recover from the activity and excitement caused by capture from the acclimation tanks. An entry device was constructed to meet these requirements (Fig. 6). Basically it consisted of a large, stoppered plastic funnel. Water from the acclimation tank was pumped through the device to maintain acclimation temperatures. Variations in ambient air temperatures and temperatures in the active capacity tunnel prevented precise control of entry device temperatures. In most cases, control was maintained within ±0.5°C.

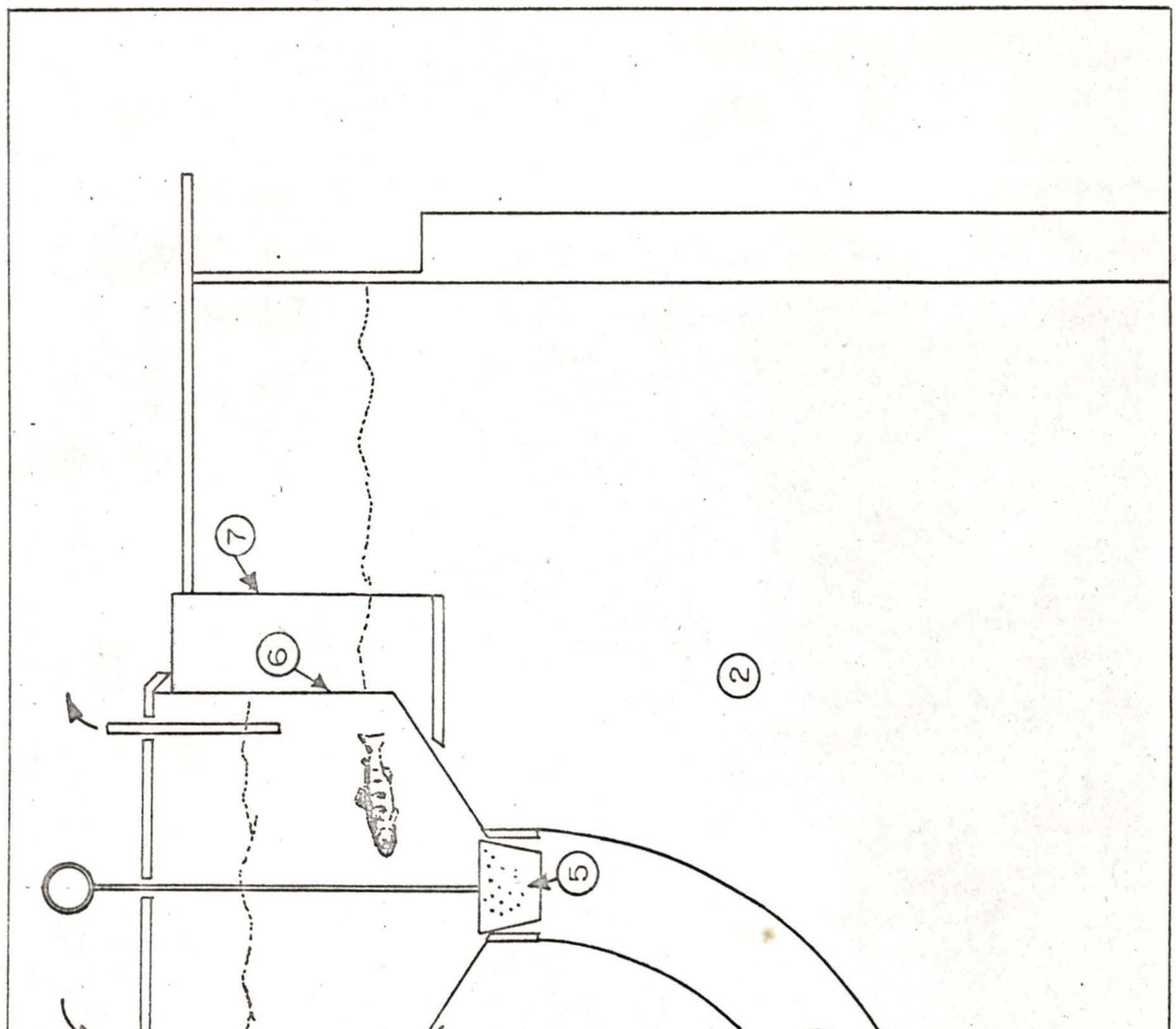
Fish were transferred from the acclimation tanks to the entry device in semi-darkness to reduce excitement and then allowed one hour to recover in the darkened entry device. The stopper was then removed and the fish were allowed to swim down the connecting tube and into the test chamber. Once the fish became quiet, the entry device was removed and the nylon screen was placed at the rear of the test chamber.

While water velocities were low, during the first few hours of a test, the fish often moved restlessly about the test chamber. A low shocker voltage (about 2 volts) was sufficient during this time to

Figure 6

Details of the entry device.

1. test chamber
2. recovery chamber
3. flexible tube
4. stainless steel screen
5. stopper
6. funnel
7. supporting bracket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condition the fish to avoid the rear of the chamber. As water velocities approached fatigue levels, the shocker device was adjusted upward to 6 volts.

Oxygen concentrations in the test water were determined (Winkler method, Strickland and Parsons, 1965) at the beginning and end of each experiment. Attempts were made to maintain oxygen concentrations at saturation levels (±5%). An air breaker in the recovery chamber prevented oxygen levels from falling much below saturation. When tests were conducted at high temperatures, it was necessary to allow adequate time for excess oxygen to be removed from the heated water. This period varied between 12 and 24 hours, depending upon the test temperature and ambient water temperature.

Fish were recovered individually as they fatigued and were swept against the rear screen. A fish was judged fatigued when gentle prodding would not remove it from the screen and restore it to swimming. The screen was then lifted and the fish was recovered, anaesthetised in MS 222, weighed and measured (total length). After the completion of a test, the fish were placed in a mesh basket in the acclimation tank for at least 12 hours. Any post-fatigue mortality was recorded. After this period, they were transferred to the "used-fish" tank.

Factor Space

The temperature tolerance range of O. kisutch spans about 25°C (0°C to 25°C). Three degree acclimation and test temperature increments were considered necessary in order to assess the effects of temperature on swimming speed. The upper acclimation limit was set at 23°C and the lower limit was set at 2°C. Test temperatures ranged from 2°C to 27.5°C.

Initial tests were conducted at points along the equal acclimation temperature-test temperature diagonal (Table II). The coho cruising speeds determined by Brett et al. (1958) were used as pre-test performance estimates (for establishing velocity increments) in this initial series of tests. Once the diagonal series was completed, adequate information was available to make reasonable pre-test estimates for subsequent experiments.

Two replicates of the factor space were determined, (Tables II and III). These could not be considered as true replicates, as sequential testing of each acclimation group was employed. Therefore, the replicates were designated as test series 1 and 2. In the analysis of the data, the experiments performed on the equal AT - TT (acclimation temperature - test temperature) diagonal were added to series 1. Some temperature combinations resulting in extreme stress were omitted in series 2, as the data from the first series indicated that the fish were incapable of performing effectively under these conditions.

A third series of tests was performed to provide information regarding the effect of size on swimming speed at different levels of acclimation and test temperatures. The 3^3 factorial design (Table IV) employed three levels of acclimation temperature, test temperature, and size.

Time limitations made it necessary to perform experiments at night as well as during the day in series 2 and 3. It was suspected that some differences in swimming ability might result from daily metabolic cycles. Therefore, a final series of tests was performed to estimate possible differences between day time and night time swimming speeds. These experiments (Table V) also gave an estimate of the variability to be expected from repeated tests under identical conditions of acclimation temperature, test temperature and size.

Analysis of Data

Individual tests.

In this study it was decided that biological variability could be best accommodated by measuring the response of a group, rather than by measuring the response of one individual. Measurements on a series of individual test fish could not be achieved in the time available. Preliminary experiments with yearling coho (11 cm in length) indicated that up to 10 fish of this size could be tested without undue crowding in the entry device or test chamber. Therefore, groups of 10 fish were used for all experiments.

When the performance of groups of fish has been measured, various estimates of the average response have been used. Davis et al. (1963) used the velocity at which first and second failures occurred in a sample of 5 fish. They suggested that the remaining fish appeared to take advantage of eddies in the test chamber, so later failure velocities were not valid indices of performance. Also, as fatigued fish could not be readily removed from the downstream screen in the apparatus these authors employed, water velocities through the chamber would decrease as the fatigued fish would partially block the screen.

Brett (1965, 1967) tested groups of from 3 to 5 sockeye underyearlings. Each individual was removed with forceps from the respirometer when it was fatigued. Brett suggests that this technique

Table II. Tests on the acclimation-test temperature diagonal and test series 1.

Diagonal:

Temperatures (AT=TT) (°C)	Mean length ± 1 standard deviation length (cm)	s.d. (cm)
11, 14, 8, 17, 5, 2	8.35	0.42

Test series 1.

Acclimation temperature (°C)	Test temperature (°C)	Mean length ± 1 standard deviation length (cm)	s.d. (cm)
23	5, 8, 11, 14, 17, 20, 23, 26, 27.5	7.52	0.22
20	2, 5, 8, 11, 14, 17, 20, 23, 26	7.90	0.28
17	2, 5, 8, 11, 14, 20, 23, 26	8.49	0.28
14	2, 5, 8, 11, 14, 17, 20, 23	7.78	0.17
11	2, 5, 8, 11, 14, 17, 20, 23	7.47	0.17
8	2, 5, 8, 11, 14, 17, 20, 23	7.56	0.14
5	2, 5, 8, 11, 14, 17, 20, 23	7.47	0.20
2	2, 5, 8, 11, 14, 17, 20	7.53	0.33

The tests in this table were carried out during the period September 19, 1968 to February 6, 1969. A mean length of 7.77 cm ± 0.43 was observed for all fish in this series.

Table III. Factor levels for test series 2.

Acclimation temperature (°C)	Test temperature (°C)	Mean length ± 1 standard deviation	
		length (cm)	s.d.(cm)
23	5, 8, 11, 14, 17, 20, 23, 26	9.44	0.17
20 *	5, 8, 11, 14, 17, 20, 23, 26	9.13	0.17
17	2, 5, 8, 11, 14, 17, 20, 23, 26	9.66	0.31
14	2, 5, 8, 11, 14, 17, 20, 23	9.26	0.22
11	2, 5, 8, 11, 14 17, 20, 23	9.21	0.28
8	2, 5, 8, 11, 14, 17, 20, 23	8.91	0.17
5	2, 5, 8, 11, 14, 17, 20, 23	9.29	0.26
2	2, 5, 8, 11, 14, 17, 20	9.39	0.22

Experiments in this series were performed during the period January 30, 1969 to April 11, 1969. A mean length of 9.29 cm ± 0.31 was observed for all fish in this replicate.

*The 20°C acclimation was repeated at the end of the series and the results of the first acclimation discarded. The initial group contracted a fungus disease and their performance was considered atypical.

Table IV. Factor levels for test series 3.

Acclimation temperature (°C)	Test temperature (°C)	Mean length ± 1 standard deviation	
		length (cm)	s.d. (cm)
5	5, 14, 23	7.06	0.44
5	5, 14, 23	8.71	0.47
5	5, 14, 23	10.73	0.28
14	5, 14, 23	7.29	0.52
14	5, 14, 23	9.03	0.28
14	5, 14, 23	10.97	0.34
23	5, 14, 23	7.32	0.48
23	5, 14, 23	9.13	0.28
23	5, 14, 23	10.96	0.40

These tests were performed during the period April 14, 1969 to April 25, 1969. Mean lengths for each size group were:

Small 7.21 ± 0.50
Medium 8.96 ± 0.40
Large 10.89 ± 0.36

Table V. Factor levels for repeated tests

Acclimation temperature (°C)	Test temperature (°C)	Time	Number of tests
14	14	Day	4
14	14	Night	4

This group of experiments was done during the period May 7, 1969 to May 13, 1969.
Mean length for all fish in these experiments was 9.58 cm ± 0.30.

occasionally caused excitement among the remaining fish. Fatigue velocities of all the fish in each sample were averaged in his studies.

The velocity profile for the water tunnel used in this study indicates that areas of reduced velocity in the test chamber were extremely small. The rear screen could be lifted easily and fatigued fish removed without disturbing those remaining. Therefore, it was considered that the failure velocities of all ten fish could be used to estimate a median failure velocity for each experiment.

Brett (1967) has shown that the distribution of fatigue times in fixed velocity experiments is similar to bioassay dosage-response data. The time to 50% fatigue could therefore be determined graphically by probit analysis (Bliss, 1937; Litchfield and Wilcoxon, 1949).

In the present study, the logarithms of the fatigue velocities for a given group of fish appeared to have a normal distribution. Probit analysis was used to estimate graphically the median failure velocity for each sample. The systematic error inherent in graphical analysis of small samples was corrected by computing the cumulative percentage fatigue as the total number responding at all lower velocities plus one-half of those responding at the velocity in question (Bliss, 1937; p. 826).

Two methods appeared possible for plotting the velocity-probit data. The first method involved plotting the logarithm of fatigue velocity (cm/second) against the cumulative % fatigued (probit units) to provide an estimate of median failure velocity in centimeters/second.

If it could be assumed, however, that size variations within a given sample were large enough to affect the order of fatigue, plotting logarithms of individual velocities in lengths/second (determined according to each individual's length) against probits of fatigue would provide a better fit to the rectilinear form.

In order to select the better method, "g" statistics (Bliss, 1937) were computed for a sample of 7 tests picked at random from all the data. The g_1 statistic (measuring skewness) is a measure of the symmetry of the distribution and the g_2 statistic (measuring kurtosis) determines whether it is actually a normal distribution. In addition to the g statistics, correlation coefficients (Li, 1964) were computed for each method to provide a measure of the scatter about the probit lines. The results of these tests (Table VI) indicate that either method would be satisfactory. However, the former method (one) generally produces better results as g_1 and g_2 are generally smaller indicating reduced skewness and kurtosis and r is generally larger, indicating reduced scatter about the probit lines. Consequently, the former method (plotting log. velocity in cm/sec. against probits of fatigue) was used to estimate the median performance. These results were divided by the appropriate mean sample lengths to convert the data to body lengths/second.

The probit transformation served to linearize most of the data, but was not entirely satisfactory in all cases. Approximately 12% of the test results showed evidence of truncated probability distributions. The departures from linearity in these cases (Fig. 7) appeared to be great enough to warrant the fitting of "split probit" lines. Median performance was then estimated from this split plot.

Table VI. Suitability of two methods of estimating median performance.

Temperature (°C)		Method 1 (log. cm/sec. vs. probits of fatigue)			Method 2 (log. lengths/sec. vs. probits of fatigue)		
AT	TT	g_1/Sg_1	g_2/Sg_2	r	g_1/Sg_1	g_2/Sg_2	r
2	2	0.263	0.303	0.978 **	0.919	0.586	0.657*
17	14	0.447	0.565	0.974 **	1.320	0.550	0.798**
2	20	3.970**	6.070 **	0.778 **	3.870 **	5.830 **	0.754**
23	8	1.077	1.006	0.907 **	0.651	1.260	0.888**
5	17	0.528	0.577	0.961 **	8.49 **	1.77	0.957**
5	14	0.371	0.591	0.968 **	1.047	0.841	0.932**
14	14	0.834	0.050	0.981 **	1.630	1.510	0.920**

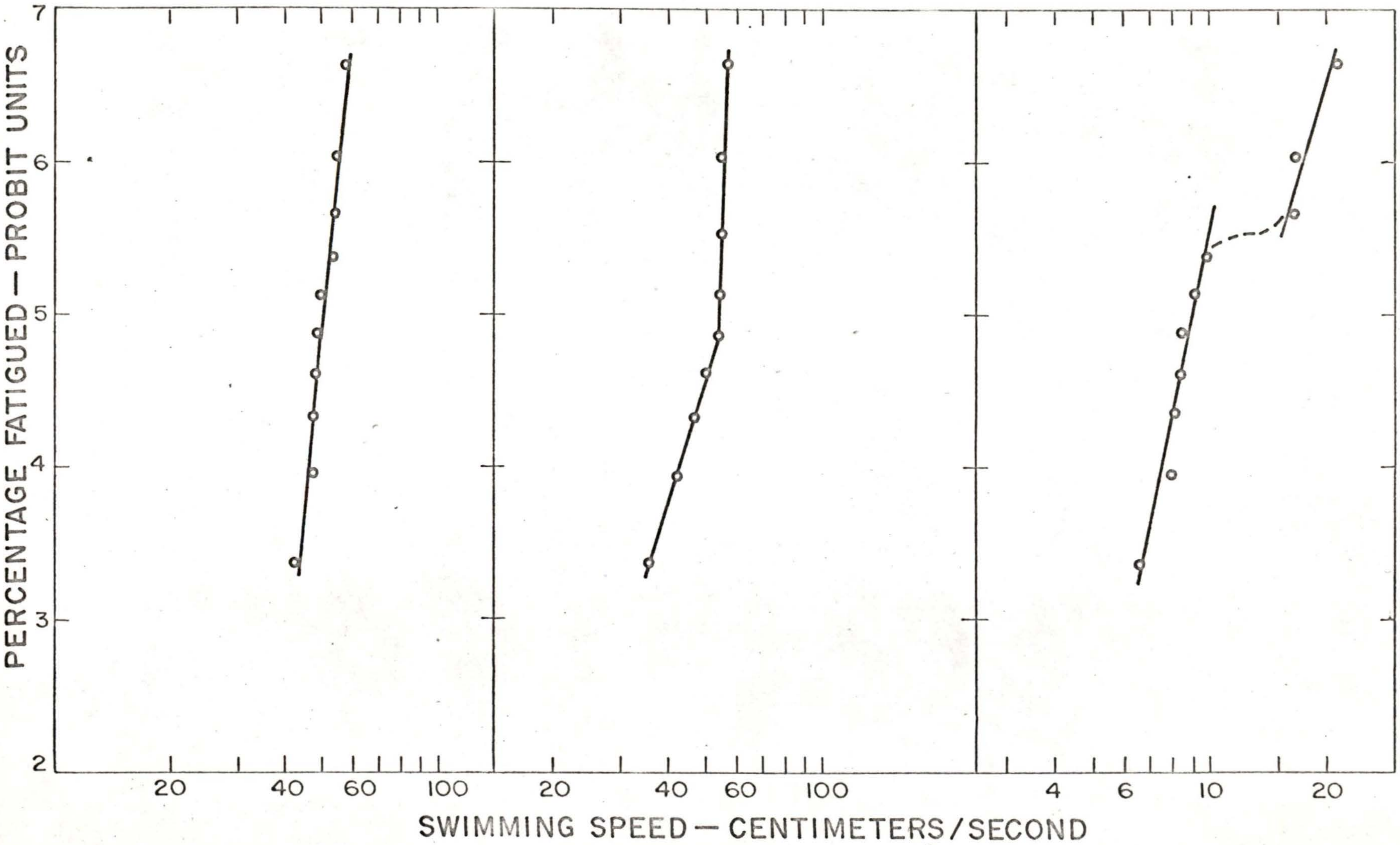
Significance levels:
the columns g/Sg are t-test for g = 0. A significant t-test indicates skewness or kurtosis. Degrees of freedom are infinite.

regression coefficient (r) has 8 degrees of freedom.

* P = 0.05
** P = 0.01

Figure 7

Examples of truncated probability distributions in swimming speeds. A normal distribution, observed in most tests, is shown for comparison.


PERCENTAGE FATIGUED — PROBIT UNITS
7
6
5
4
3
2
20
40
60
100
20
40
60
100
4
6
10
20
SWIMMING SPEED — CENTIMETERS/SECOND

While this method has obvious shortcomings, it appeared superior to the fitting of single straight lines to data which was obviously non-linear.

Calibration correction of test series 1.

A calibration check on the active capacity apparatus following completion of the first test series indicated that water velocities produced at a given propellor R.P.M. were 32% lower than when the apparatus was first calibrated. This error was caused by an accumulation of detritus on the turbulence screens and its re-occurrence was prevented by regular cleaning of these screens. However, it was necessary to apply an objective correction to the data obtained before discovery of the calibration error.

The calibration error was known to be 0% at the time of the first experiments and 32% at the time test series 1 was completed. No direct information was available regarding the time at which a significant error first occurred, or the rate at which it increased.

An indirect method of correction was employed. Two estimates of swimming speed were available (Table II) for those points in the factor space where acclimation and test temperatures were equal. The results of the equal AT-TT diagonal series could be considered free of calibration errors as these tests were completed shortly after the initial calibration. The results of corresponding points from each acclimation group in test series 1 would be subject to varying degrees of error, according to the calibration error at the time of testing. Comparison of these two sets of results provided a measure of the calibration error at the time each acclimation group was tested. The comparison was made not between pairs of observed results, but between points on a curve fitted to the results for the initial tests performed on the temperature diagonal and corresponding points on curves fitted to the results from each acclimation group. The errors for each acclimation group were plotted with respect to the chronological order of testing and a curve was fitted by eye to this data (Fig. 8). This curve was used to determine a percentage correction for each acclimation group in test series 1 and the corrected data was used for all subsequent calculations. The calibration error at the end of the series was 31% as determined by this method, and agrees well with the actual error observed at this time.

Analysis of test series 1, 2 and 3.

The estimates of median swimming velocity were used to develop response surfaces for the effect of acclimation and test temperatures on swimming speed. The method of analysis was initially described by Box (1956) and involves fitting a quadratic polynomial to the data. Using a computer program (Lindsey, 1968), both linear and non-linear response surfaces were calculated.

The two-factor surfaces (test series 1 and 2) were fitted with a linear model:

$$Y = b_o x_o + b_1 x_1 + b_2 x_2 + b_{11} x_1^2 + b_{22} x_2^2 + b_{12} x_1 x_2$$

where x_1 = acclimation temperature, °C.

x_2 = test temperature, °C.

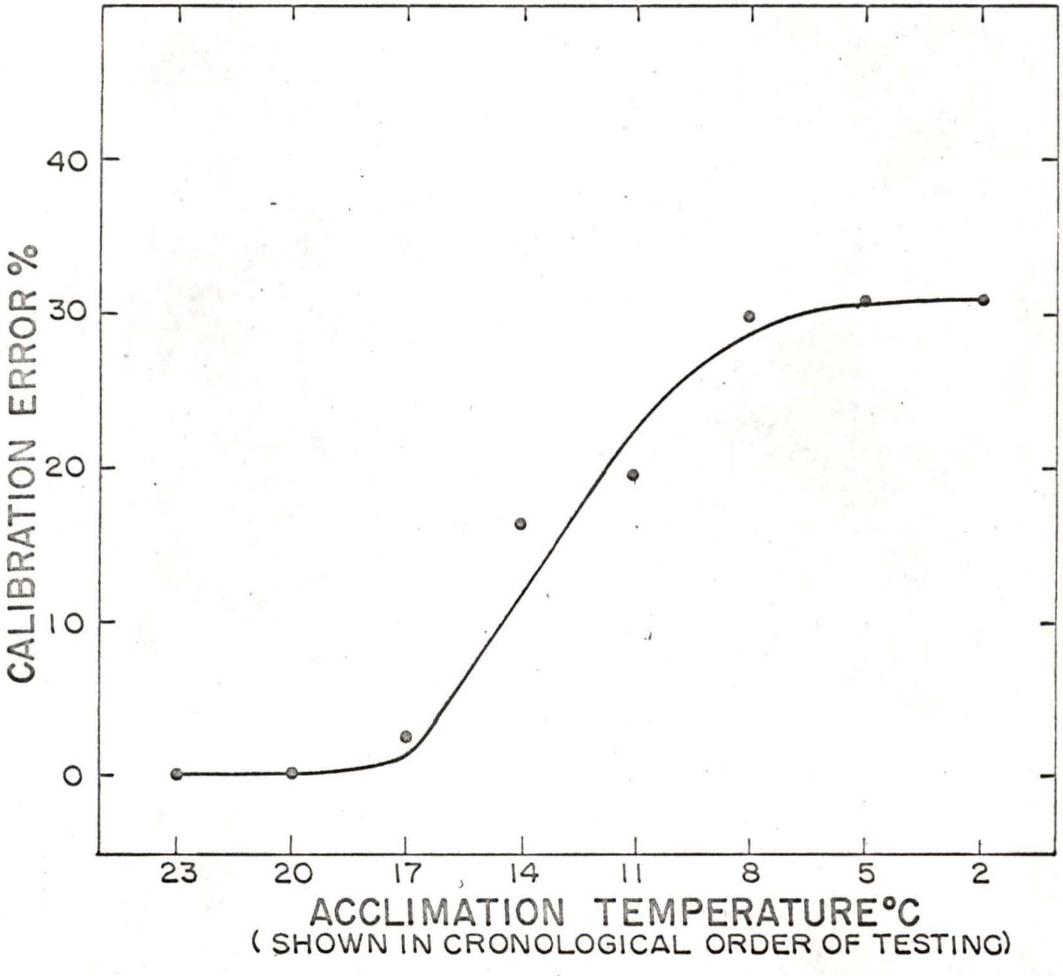
Y = critical swimming speed, lengths/second.

The non-linear model involved transformations of the independent variables (x_1 and x_2) and the dependent variable (Y) as described by Lindsey et al. (MS). The transformed polynomial was:

Figure 8

The curve used to correct calibration errors in

test series 1.


CALIBRATION ERROR %
40
30
20
10
0
23
20
17
14
11
8
5
2
ACCLIMATION TEMPERATURE °C
(SHOWN IN CRONOLOGICAL ORDER OF TESTING)

$$Y^{\gamma} = b_o x_o + b_1 x_1^{\alpha_1} + b_2 x_2^{\alpha_2} + b_{11} x_1^{2\alpha_1} + b_{22} x_2^{2\alpha_2} + b_{12} x_1^{\alpha_1} x_2^{\alpha_2}.$$

The power parameters (α_1, α_2 and γ) were determined. Maximum likelihood ratios were calculated to provide a measure of the precision of the estimates. The precision of the centre points for both the linear and non-linear models was similarly calculated.

The data of test series 3 was fitted with a three-factor response surface, again using the program of Lindsey (1968). The linear model was:

$$Y = b_o x_o + b_1 x_1 + b_2 x_2 + b_3 x_3 + b_{11} x_1^2 + b_{22} x_2^2 + b_{33} x_3^2 + b_{12} x_1 x_2 + b_{13} x_1 x_3 + b_{23} x_2 x_3$$

where x_1 = acclimation temperature, °C.

x_2 = test temperature, °C.

x_3 = size, cm.

Y = critical swimming speed, lengths/second.

As in the two factor case, a transformed polynomial was calculated to provide a non-linear model for the effects of acclimation temperature, test temperature and size on swimming speed. The non-linear model was:

$$Y^{\gamma} = b_o x_o + b_1 x_1^{\alpha_1} + b_2 x_2^{\alpha_2} + b_3 x_3^{\alpha_3} + b_{11} x_1^{2\alpha_1} + b_{22} x_2^{2\alpha_2} + b_{33} x_3^{2\alpha_3} + b_{12} x_1^{\alpha_1} x_2^{\alpha_2} + b_{13} x_1^{\alpha_1} x_3^{\alpha_3} + b_{23} x_2^{\alpha_2} x_3^{\alpha_3}.$$

The fitted linear and non-linear response surfaces were used to determine the dimensions of the coho's active capacity domain and the position of its performance optimum within this domain, in relation to the variables, acclimation temperature, test temperature and size. Contour plots were employed, showing isopleths of swimming speed in relation to quantitative changes in these 3 variables.

RESULTS

Test Series 1 (September 19, 1968 to February 6, 1969

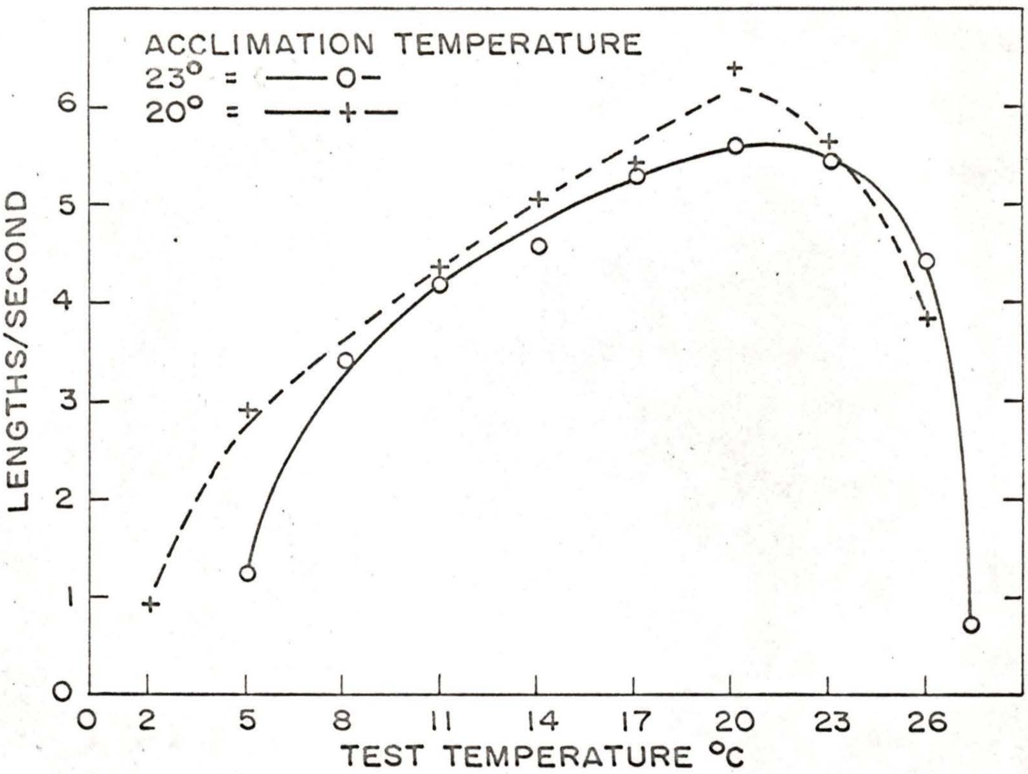
Fitting a response surface by eye.

Lines of best fit were drawn by eye through the data from each acclimation group in test series1(Figs. 9 and 10). These curves represent transects taken at 3°C. intervals of acclimation temperature across the response surface relating acclimation temperature and test temperature to swimming speed (Fig. 11). The transects in Figs. 9 and 10 are shown by the solid lines in Fig. 11. As illustrated by the broken lines in Fig. 11, a second series of transects was constructed from the data, relating acclimation temperature to performance at different levels of test temperature. Diagonal transects of the response surface were also plotted.

While the three-dimensional plot indicates the general nature of the response surface, its actual shape in relation to the acclimation and test temperature axes is difficult to visualize. A contour plot (Fig. 12) of the response surface was constructed to aid interpretation. From each transect, those combinations of acclimation and test temperatures were estimated which produced a given level of response. For example, at an acclimation temperature of 20° C. (Fig. 9) a swimming speed of 5.0 lengths/second would be expected at test temperatures of 14° C. and about 24.5°C. A number of loci in the factor space producing this level of response were determined by examination of all the transects of the surface. These loci indicated the position of a 5.0 lengths/second response isopleth on the surface. Isopleths for response levels of 6.0, 5.5, 5.0, 4.5, 4.0, 3.5, 3.0, 2.5 and 2.0

Figure 9

Test series 1. The effects of test temperature on swimming speeds of juvenile coho at various acclimation temperatures. Lines of best fit are drawn by eye.


ACCLIMATION TEMPERATURE
23° = —O—
20° = —+—
LENGTHS/SECOND
0
1
2
3
4
5
6
0
2
5
8
11
14
17
20
23
26
TEST TEMPERATURE °C

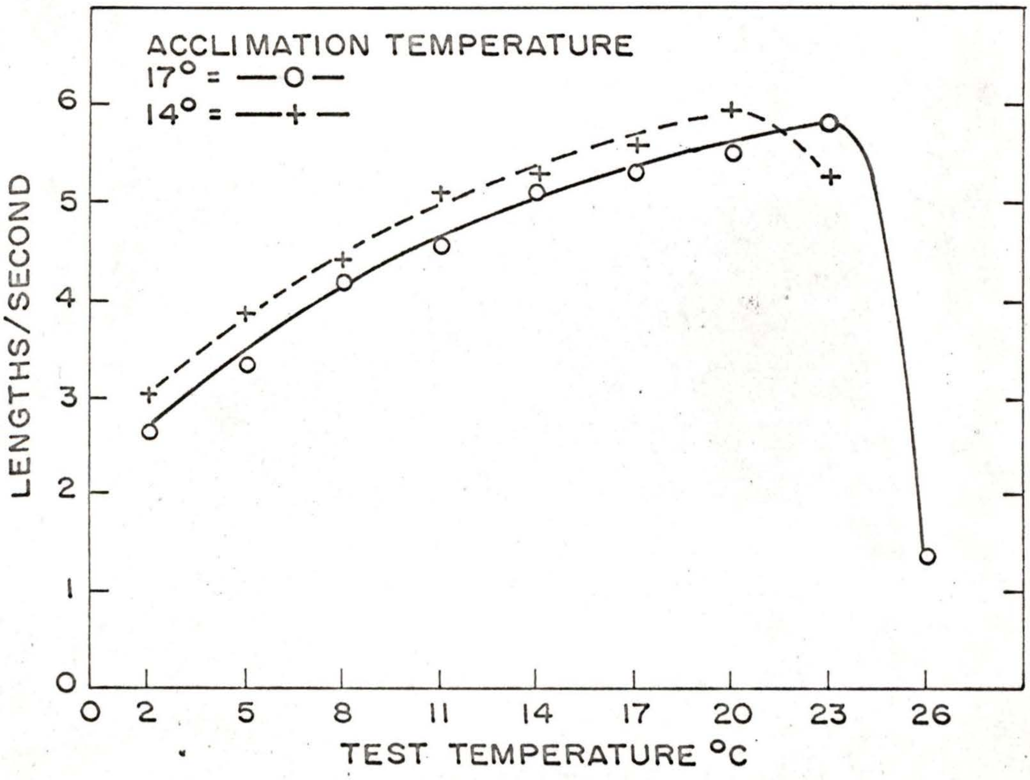
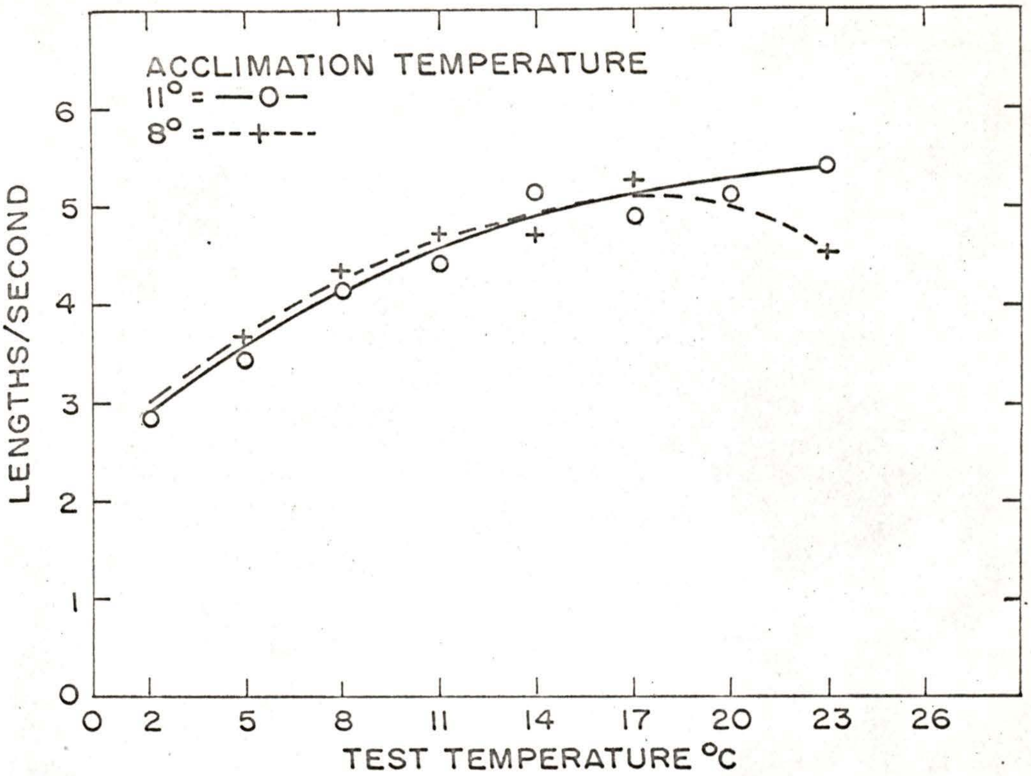

ACCLIMATION TEMPERATURE
17° = —O—
14° = —+—
LENGTHS/SECOND
0
1
2
3
4
5
6
0
2
5
8
11
14
17
20
23
26
TEST TEMPERATURE °C

Figure 10

Test series 1. The effects of test temperature on swimming speeds of juvenile coho at various acclimation temperatures. Lines of best fit are drawn by eye.


ACCLIMATION TEMPERATURE
11° = —O—
8° = - - + - - -
LENGTHS/SECOND
0
1
2
3
4
5
6
0
2
5
8
11
14
17
20
23
26
TEST TEMPERATURE °C

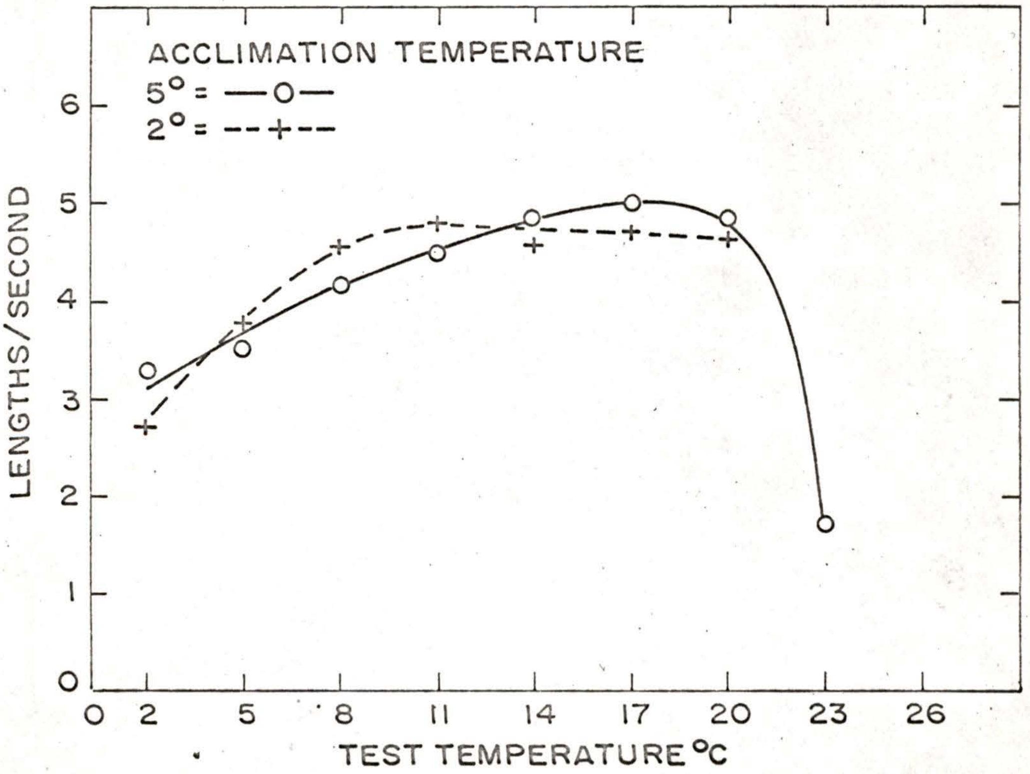

ACCLIMATION TEMPERATURE
5° = —O—
2° = - - + - -
LENGTHS/SECOND
0
1
2
3
4
5
6
0
2
5
8
11
14
17
20
23
26
TEST TEMPERATURE °C

Figure 11

Test series 1. The response surface relating acclimation temperature and test temperature to swimming speed. The curves in Figs. 9 and 10 are shown as solid lines. The dotted lines represent transects constructed from the data, relating the effect of acclimation temperature on swimming speed at each test temperature.

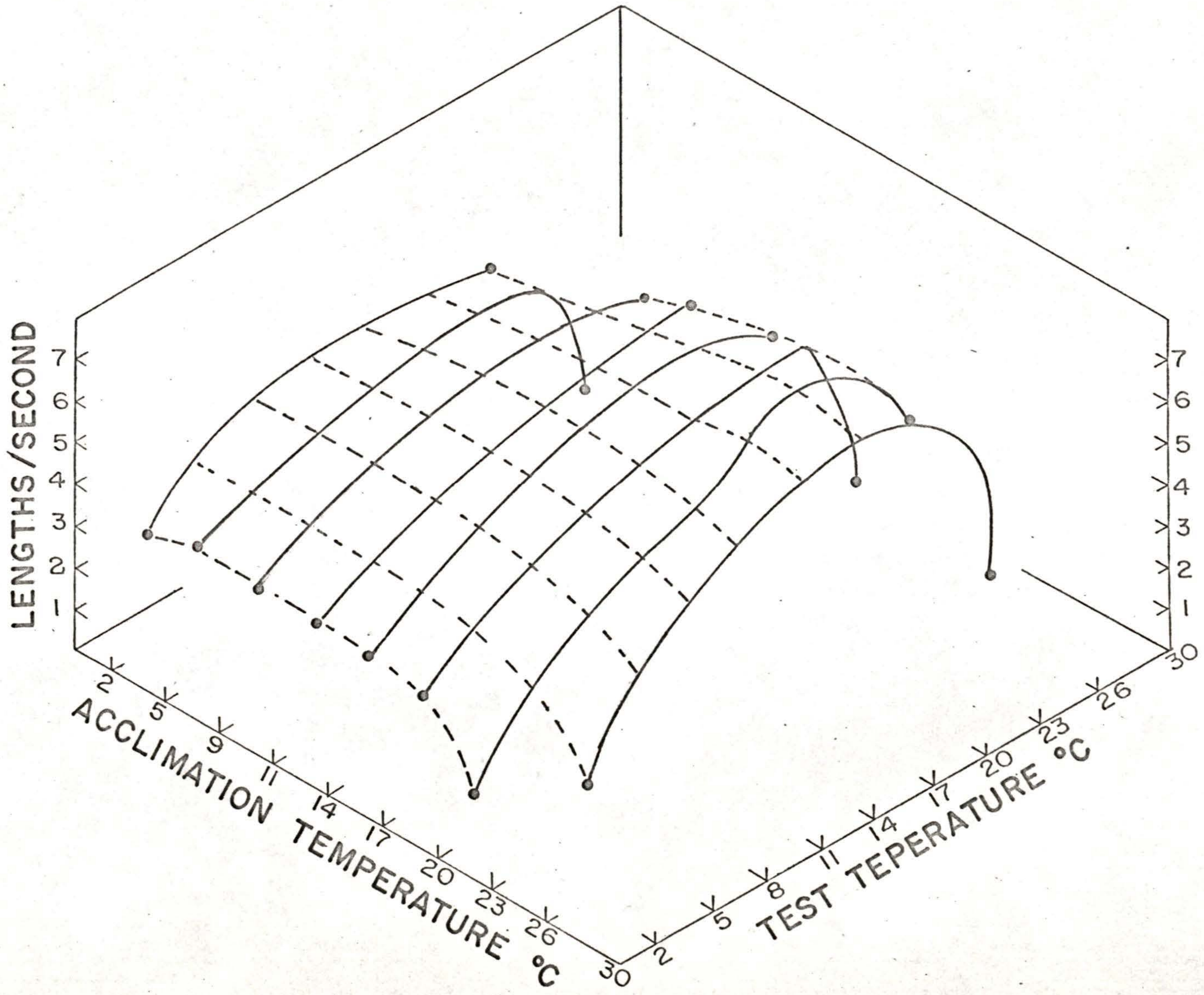
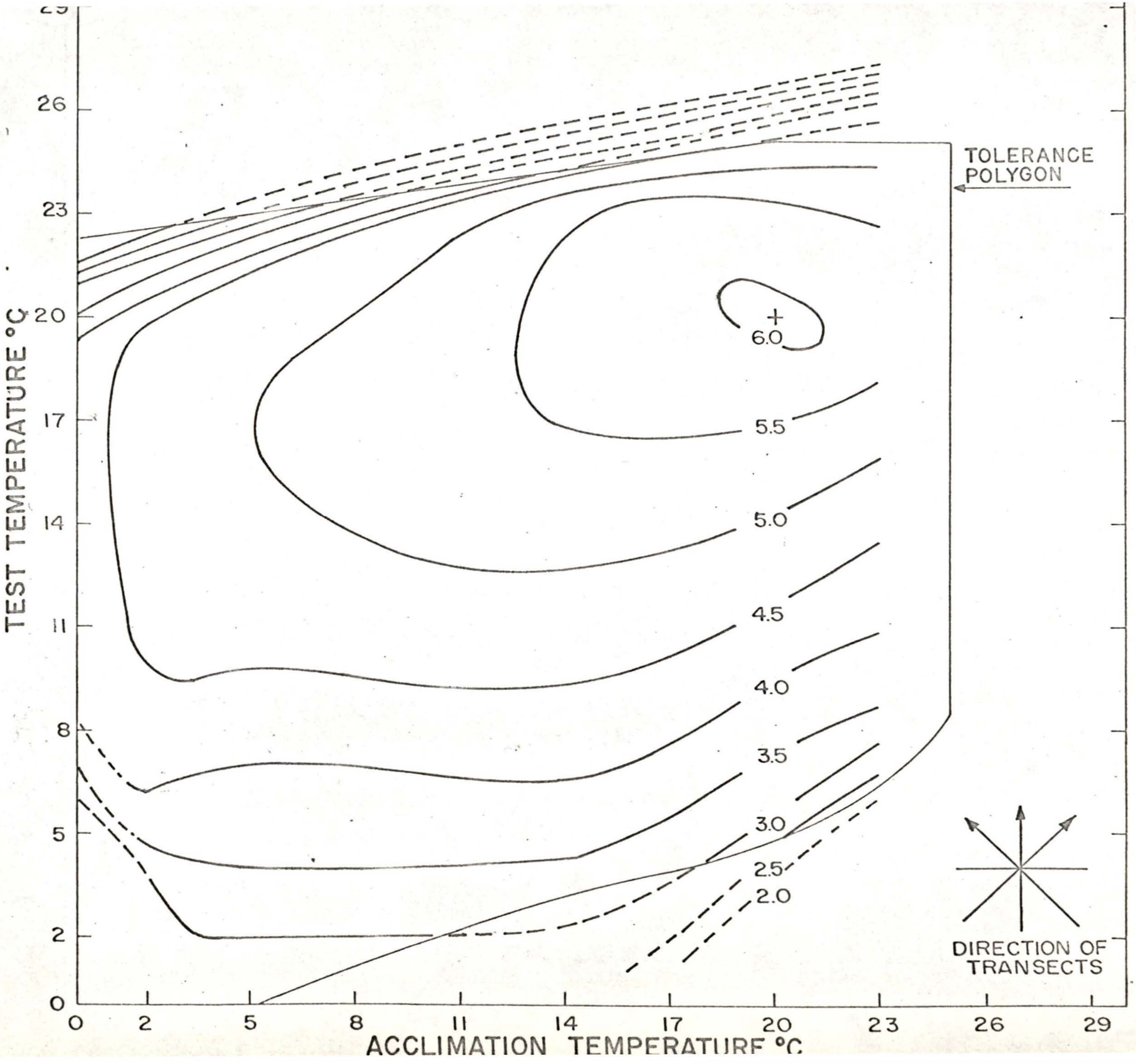

LENGTHS/SECOND
1
2
3
4
5
6
7
ACCLIMATION TEMPERATURE °C
2
5
9
11
14
17
20
23
26
30
TEST TEPERATURE °C
2
5
8
11
14
17
20
23
26
30

Figure 12

A contour plot of the response surface in Fig. 11. Response contours are isopleths of swimming speed (lengths/second). The response surface is shown in relation to the coho temperature tolerance polygon (Brett, 1952). Swimming performance observed in the zones of resistance (outside the tolerance polygon) are denoted by dotted lines. The direction of the transects used to estimate the response isopleths is indicated (see text for further explanation).


TOLERANCE POLYGON
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
DIRECTION OF TRANSECTS
TEST TEMPERATURE °C
0
2
5
8
11
14
17
20
23
26
ACCLIMATION TEMPERATURE °C
0
2
5
8
11
14
17
20
23
26
29

lengths/second were determined from the transects.

The response isopleths were plotted on the acclimation temperature-test temperature plane to produce a two-dimensional contour plot of the response surface (Fig. 12). This procedure is analagous to plotting elevations on a topographic map. The response surface contours are shown in relation to the coho temperature tolerance polygon defined by Brett (1952). Response isopleths outside the tolerance polygon are represented by dotted lines, as any ability to perform in the zone of resistance would be time-dependent and cannot be considered as a true sustained swimming speed.

The centre of the response surface (maximum swimming speed) occurred at an acclimation temperature of 20° C and a test temperature of 20° C. Elongation of the surface on the acclimation temperature axis indicates that test temperature had the greatest effect on performance. That is, there was a greater change in performance per degree of temperature change for test temperature, as compared with that for acclimation temperature. This elongation is described as a <u>rising ridge</u>. The ridge may be followed by estimating the test temperature producing maximal performance for a given acclimation temperature. This appears to be about 16° C for 2° C acclimated fish, and rises until test and acclimation temperatures coincide at about 20° C.

The response surface indicates that coho were able to perform quite well throughout most of the tolerance zone. When compared with the maximum rate, swimming speeds at the low temperature tolerance boundary were reduced by about 50 percent. The performance of warm-acclimated fish (20° C - 23° C) was very limited at test temperatures below the low temperature tolerance boundary. The reduction in swimming speed at the high temperature tolerance boundary was about 70 percent for 2° C acclimated fish, but only 30 percent for those acclimated to 23° C. Warm-acclimated coho (20° C to 23° C) were able to maintain high swimming speeds for the test period at temperatures a degree or more above the upper tolerance boundary.

Calculated response surfaces.

Linear and non-linear response surface models were fitted to the data from test series 1 (Appendix I) to further evaluate the effects of acclimation temperature (x_1) and test temperature (x_2) on swimming speed (Y). For the linear model, a second degree polynomial was fitted. Hence:

$$Y = 1.825 + 0.040x_1 + 0.434x_2 - 0.006x_1^2 - 0.017x_2^2 + 0.008x_1x_2.$$

Analysis of variance (Table VII) indicated that only the term for the linear effect of acclimation temperature could be removed without greatly affecting the adequacy of the model.

The response surface could be plotted by direct substitution into the polynomial, but it was more convenient to transform the polynomial to its canonical form (Box, 1956). The transformation involves a translocation from the centre of the design to the calculated centre of the response surface, and a rotation of the axes of measurement from those of the design to those of the response surface. Hence, the polynomial was reduced to the form:

$$Y - Y_s = \lambda_{11} X_1^2 + \lambda_{22} X_2^2$$

where Y_s = swimming speed calculated at the centre of the response surface.

λ = eigenvalues, denoting the rate at which the response changes in the direction of the X-axes (axes of the response surface).

The polynomial fitted to the series 1 data was reduced to:

$$Y - 5.47 = -0.0190X_1^2 - 0.0049X_2^2.$$

The signs of the eigenvalues indicated that the response reached a true maximum within the factor space investigated (Box, 1956). The centre of the response surface was calculated at:

acclimation temperature (x_1) = 13.62° C.

test temperature (x_2) = 15.54° C.

The calculated swimming speed at the centre (Y_s) was 5.47 lengths/second.

The centre of the calculated linear response surface is quite different from the centre shown on the surface drawn by eye. Maximum relative likelihood plots (Fig. 13) indicate that the centre point of the linear model was much more clearly defined with respect to test temperature (x_2) than to acclimation temperature (x_1). Significance levels are not tabulated for likelihood ratios, but values having a relative likelihood of less than 0.1 may be considered <u>unlikely</u> estimates of the parameters. Thus, while it is plausible that centre of the linear model may occur at an acclimation temperature as high as 20° C, it is unlikely that the centre occurs at a test temperature above 16.5° C.

The linear response surface was plotted (Fig. 14) by substitution into the canonical equation. Elongation of this surface on the X_1 -axis indicates that test temperature had a much greater effect on performance than acclimation temperature.

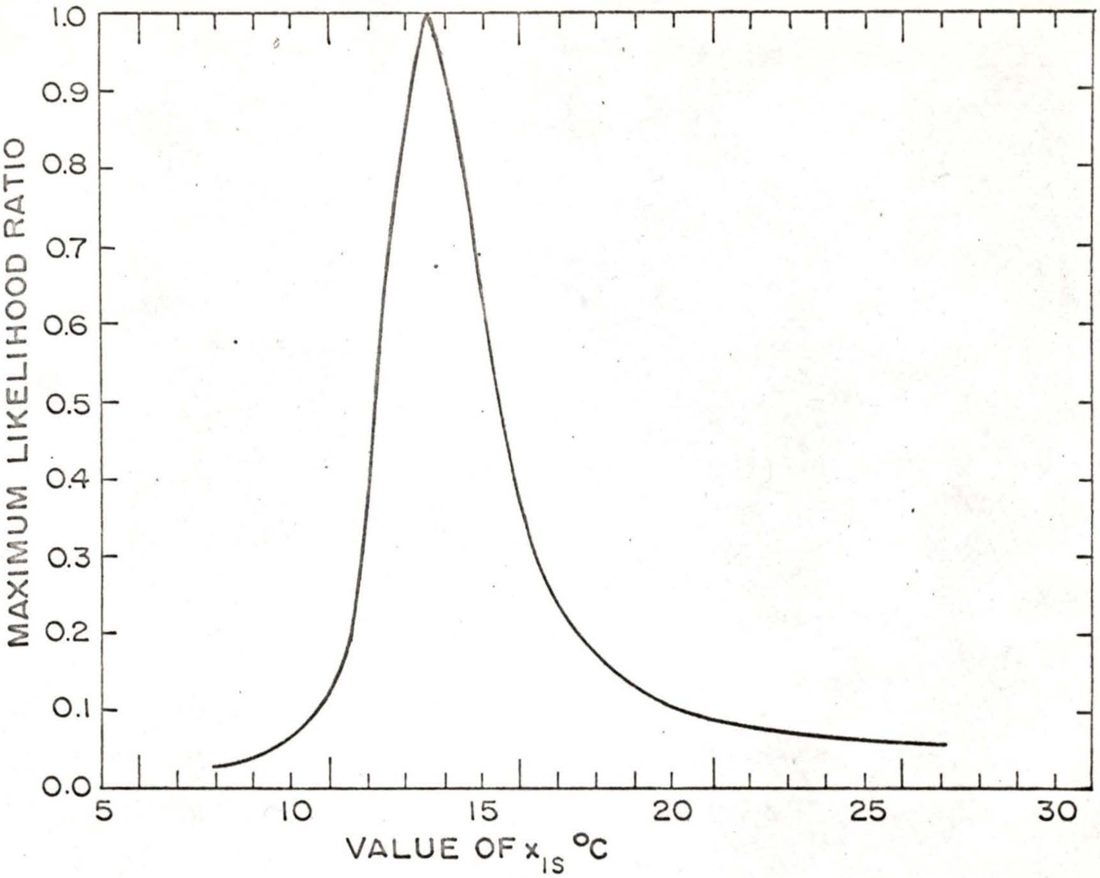
Table VII. Analysis of variance of the untransformed data from test series 1.

Source of Variation	SS	d.f.	MSS	F
Treatments	100.77	70	1.43	2.92 **
Linear	14.56	2	7.28	14.82 **
x_1 linear	0.23	1	0.23	0.47
x_2 linear	14.32	1	14.32	29.14 **
Quadratic	49.37	2	24.68	50.23 **
x_1 Quad.	4.28	1	4.28	8.71 **
x_2 Quad.	45.07	1	45.07	91.70 **
$x_1 - x_2$	9.50	1	9.50	19.33 **
Lack of fit	31.94	65	0.49	
Total	100.77	70		

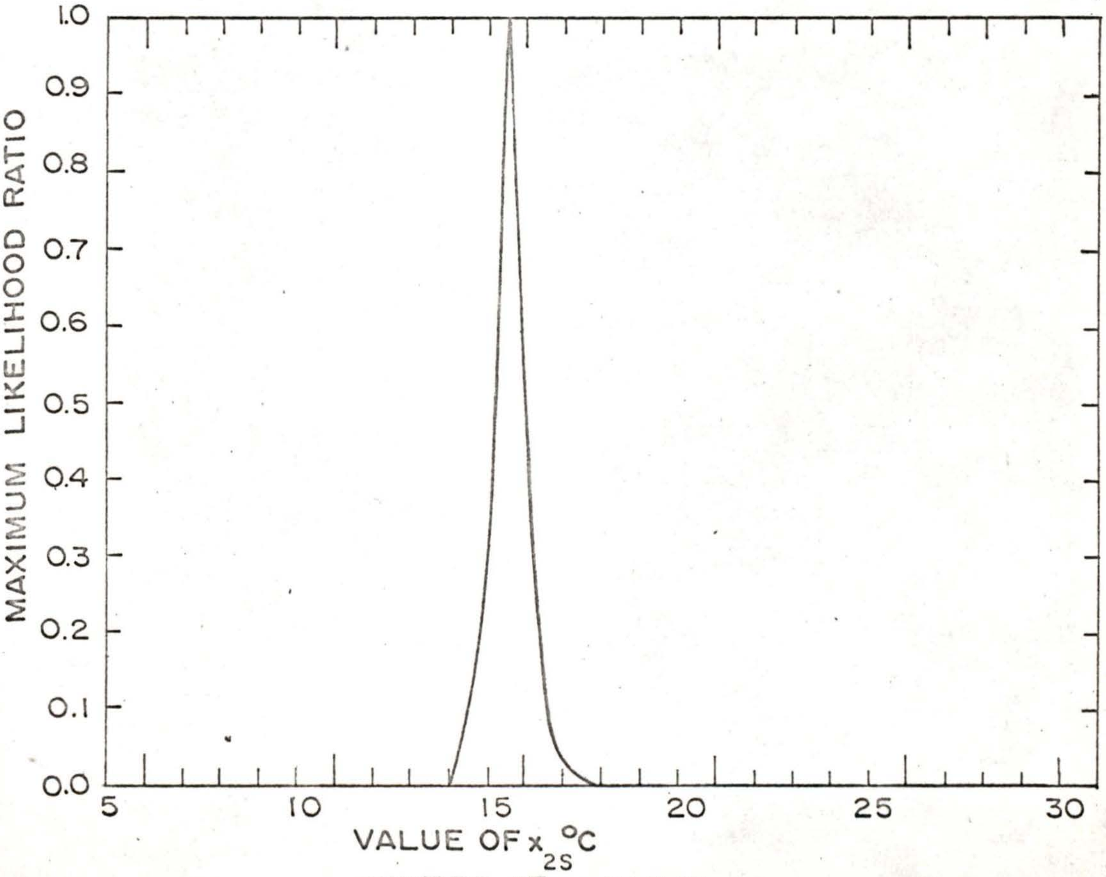
* P = 0.05
** P = 0.01

Figure 13

Test series 1. Maximum likelihood ratios of various estimates of the centre coordinates for the linear response surface model. The symbol x_{1s} denotes the acclimation temperature coordinate, x_{2s} the test temperature coordinate.



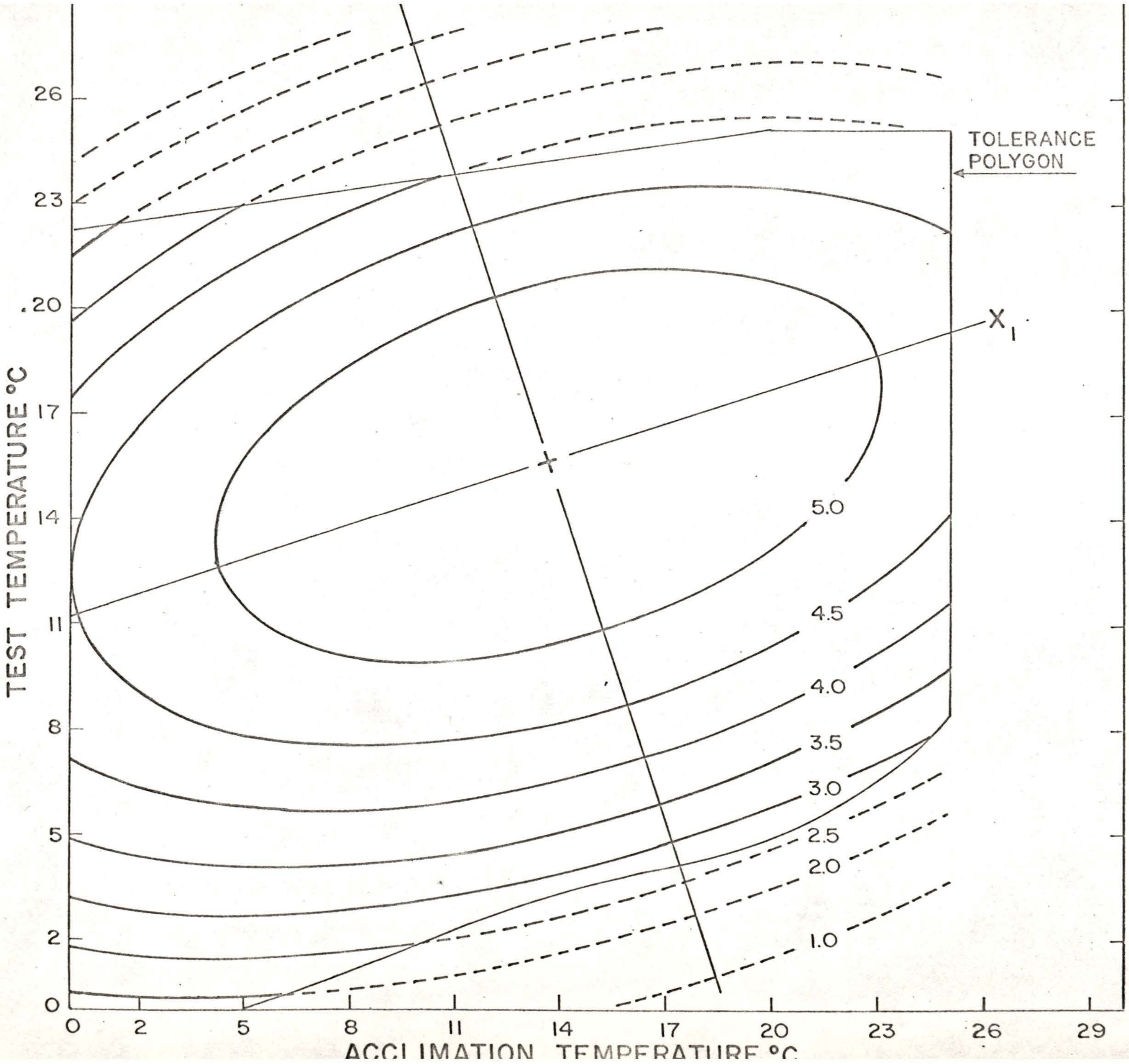
CENTRE AT x_{1S} = 13.623



CENTRE AT x_{2S} = 15.543

Figure 14.

The linear response surface fitted to the data from test series 1, shown in relation to the coho tolerance polygon (Brett, 1952). The calculated axes of the response surface are denoted by X_1 and X_2. The contours are swimming speed isopleths in lengths/second.


TOLERANCE POLYGON
X1
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.0
TEST TEMPERATURE °C
26
23
.20
17
14
11
8
5
2
0
ACCLIMATION TEMPERATURE °C
0
2
5
8
11
14
17
20
23
26
29

Interaction between acclimation temperature and test temperature is shown by the rotation of the X_1- and X_2- axes in relation to the axes of measurement.

Comparison of Figs. 12 and 14 indicates that the shape of the linear model is quite different from that of the response surface plotted by eye. The differences are most noticeable at combinations of low test and acclimation temperatures, and at test temperatures above the lethal limits.

On the basis of the differences in shape and position of the centre point of the two surfaces, the linear model does not appear adequate to describe the observed data. The significance of the deviations from regression could not be determined in the analysis of variance, as the model was calculated from a single replicate. A comparison of the linear model with a non-linear model fitted to the same data was therefore used to determine the adequacy of the linear model to describe the data.

The power parameters of the non-linear model were estimated as:

$$\alpha_1 = 1.16$$

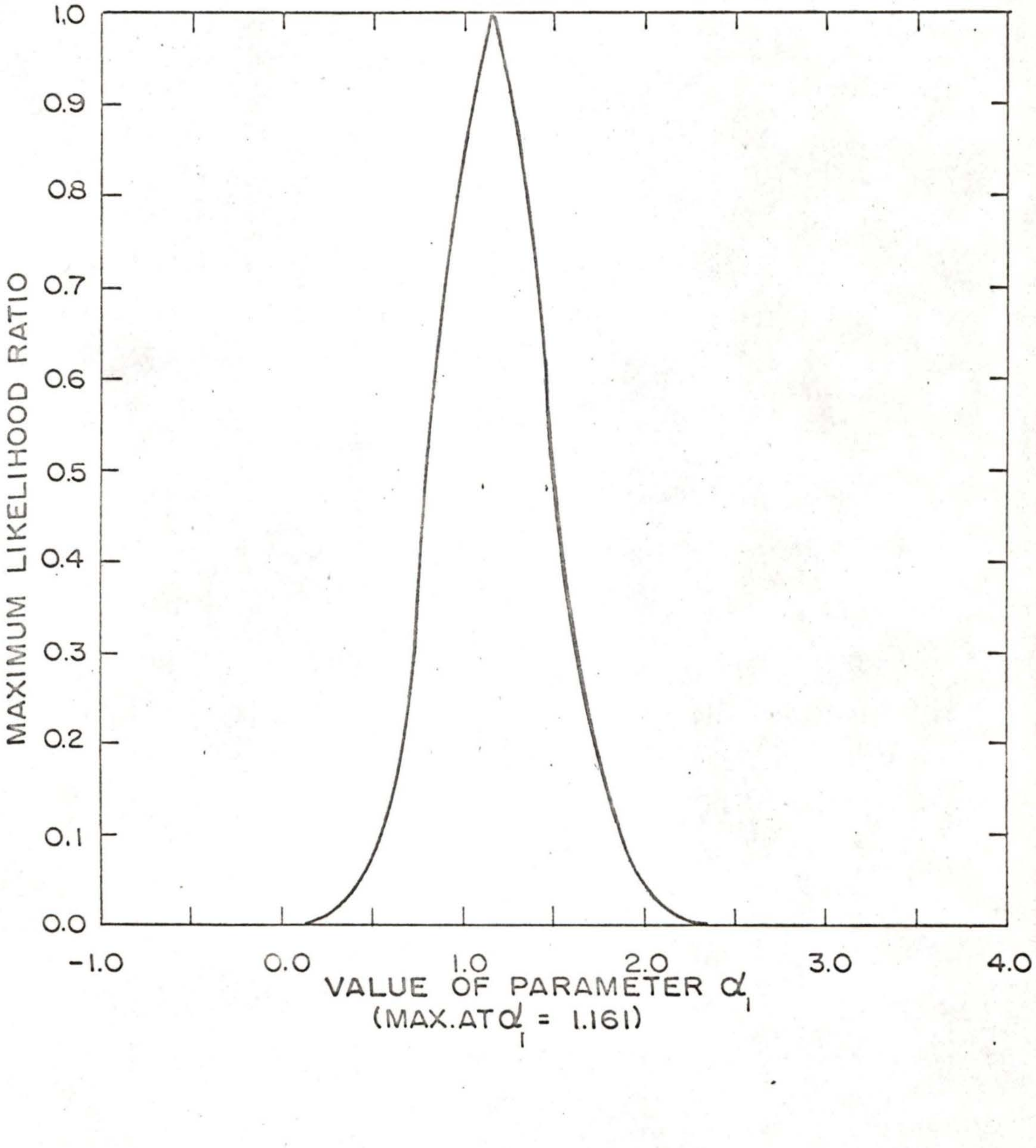
$$\alpha_2 = 2.35$$

$$\gamma = 2.37$$

The maximum likelihood ratio plots (Figs. 15, 16, 17) show that all three parameters were defined reasonably well. The effect of test temperature again was more clearly defined, as the range of plausible values for X_2 was very small.

Figure 15

Test series 1, the non-linear model: maximum likelihood ratios of various estimates of the power parameter α_1.



1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
MAXIMUM LIKELIHOOD RATIO
-1.0
0.0
1.0
2.0
3.0
4.0
VALUE OF PARAMETER α_1
(MAX. AT α_1 = 1.161)

Figure 16

Test series 1, the non-linear model: maximum likelihood ratios of various estimates of the power parameter α_2.

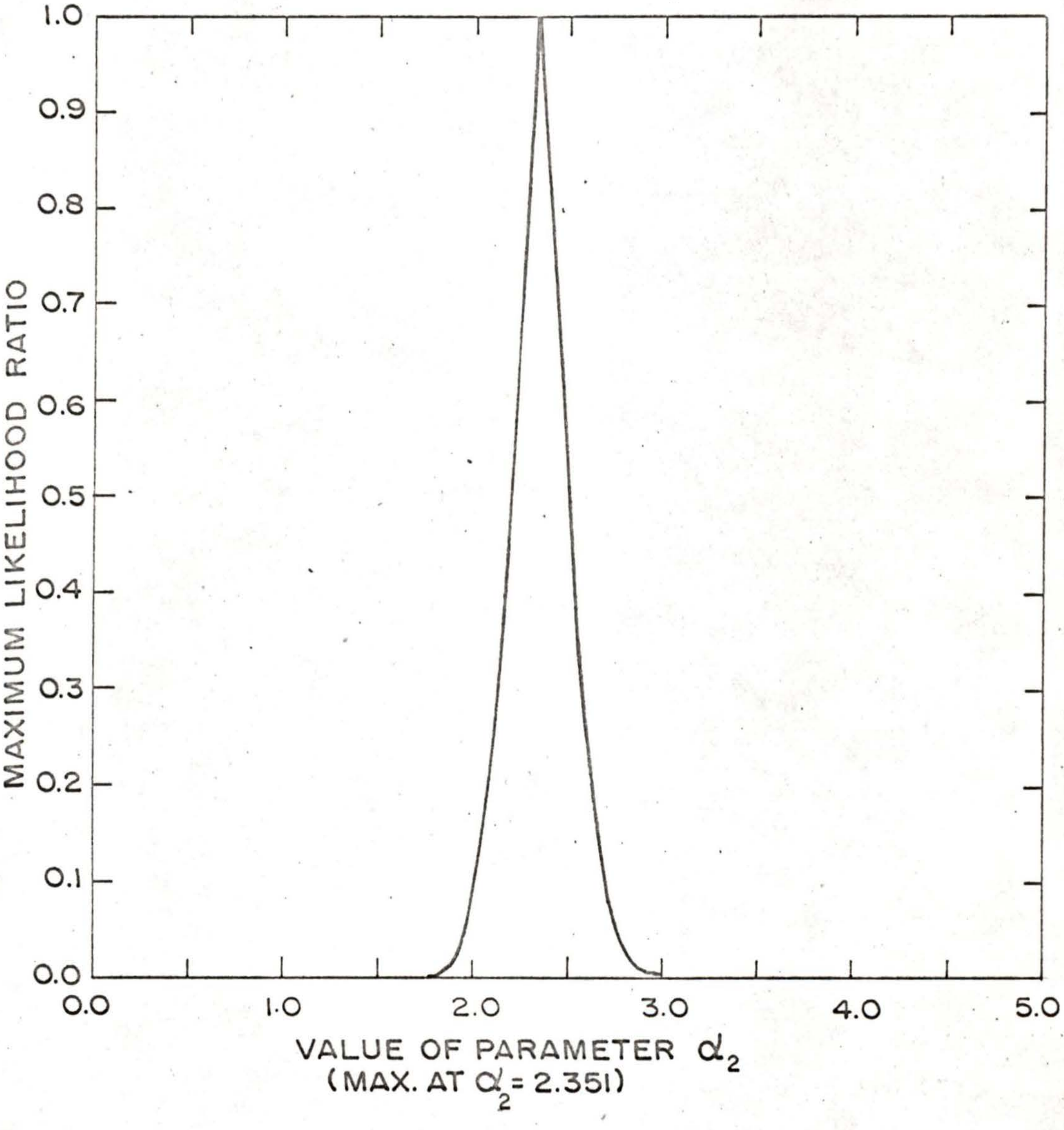
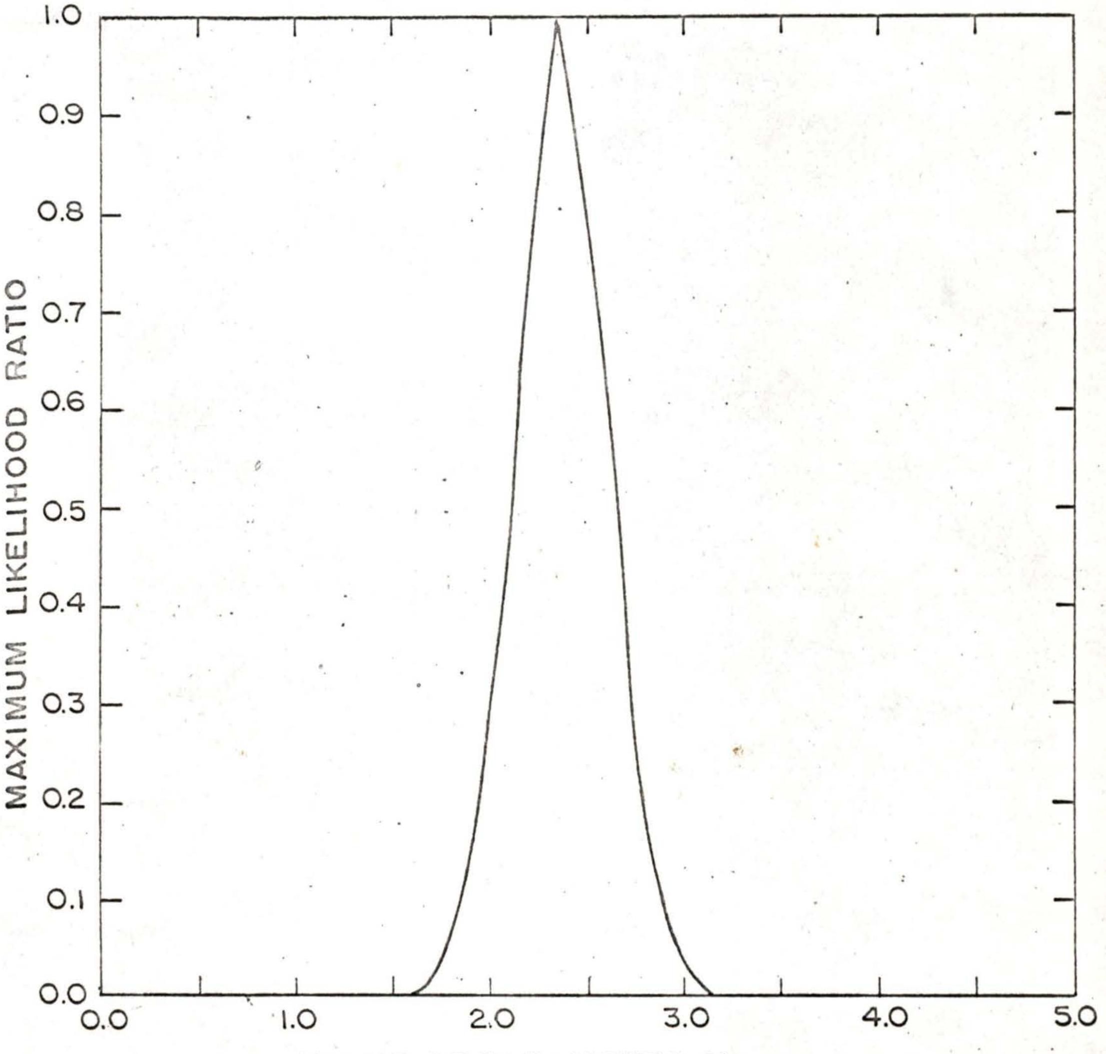

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
MAXIMUM LIKELIHOOD RATIO
0.0
1.0
2.0
3.0
4.0
5.0
VALUE OF PARAMETER α_2
(MAX. AT α_2 = 2.351)

Figure 17

Test series 1, the non-linear model: maximum likelihood ratios of various estimates of the power parameter γ.



VALUE OF PARAMETER γ
MAX. AT γ = 2.369

The polynomial,

$$Y^{2.37} = 15.527 + 0.674x_1^{1.16} + 0.063x_2^{2.35} - 0.029x_1^{2.32} - 4.0 \times 10^{-5}x_2^{4.70} + 1.2 \times 10^{-3}x_1^{1.16}x_2^{2.35}$$

was calculated from the data. The analysis of variance (Table VIII) is unusual, as true "F" ratios cannot be calculated from the transformed data (Lindsey et al., MS). Exact inferences can be drawn, however, by maximum likelihood procedure. Therefore, maximum likelihood ratios (range 0 to 1.0) were calculated (MIR column, Table VIII). These ratios indicate the likelihood of the value of the component or parameter tested being replaced by zero. Hence, the likelihood that treatment effects (temperature experience and its effects on performance) do not account for a significant proportion of the total variance is very small (Table VIII). Only the linear term for test temperature (x_2) could be removed without greatly affecting the adequacy of the non-linear model. Comparison of the likelihood ratios with the approximate "F" ratios in Table VIII is useful to familiarize oneself with the analysis of variance for the transformed data.

The canonical form of the fitted equation was calculated:

$$Y - 65.532 = -0.029X_1^2 - 0.00003X_2^2.$$

The canonical equation again provides a useful means of plotting the non-linear response surface (Fig. 18). Comparison of the non-linear plot with the response surface drawn by eye suggests that the non-linear model closely describes the observed data.

The relative likelihood of the computed linear model versus the non-linear model was calculated as 1.70×10^{-18}. Clearly, the non-linear model provides a better fit to the observed data.

Table VIII. Analysis of variance of the transformed data from test series 1.

Source of Variation	SS	d.f.	MSS	Approx. F	MIR
Treatments	87.83	70	1.25	7.71	9.13×10^{-36}
Linear	3.19	2	1.59	9.81	5.74×10^{-5}
x_1 linear	1.73	1	1.73	10.65	3.59×10^{-3}
x_2 linear	0.57	1	0.57	3.51	0.14
Quadratic	66.29	2	33.14	203.67	6.19×10^{-32}
x_1 Quad.	3.22	1	3.22	19.82	5.27×10^{-5}
x_2 Quad.	63.46	1	63.46	389.98	2.36×10^{-31}
$x_1 * x_2$	14.70	1	14.70	90.34	1.37×10^{-14}
Transform	21.85	3	7.28	44.86	1.70×10^{-18}
Lack of fit	10.08	62	0.16		
Total	87.83	70			

Figure 18

The non-linear response surface fitted to the data from test series 1. The contours are isopleths of swimming speed in lengths/second and are dotted outside the tolerance polygon. X_1 and X_2 denote the axes of this surface.

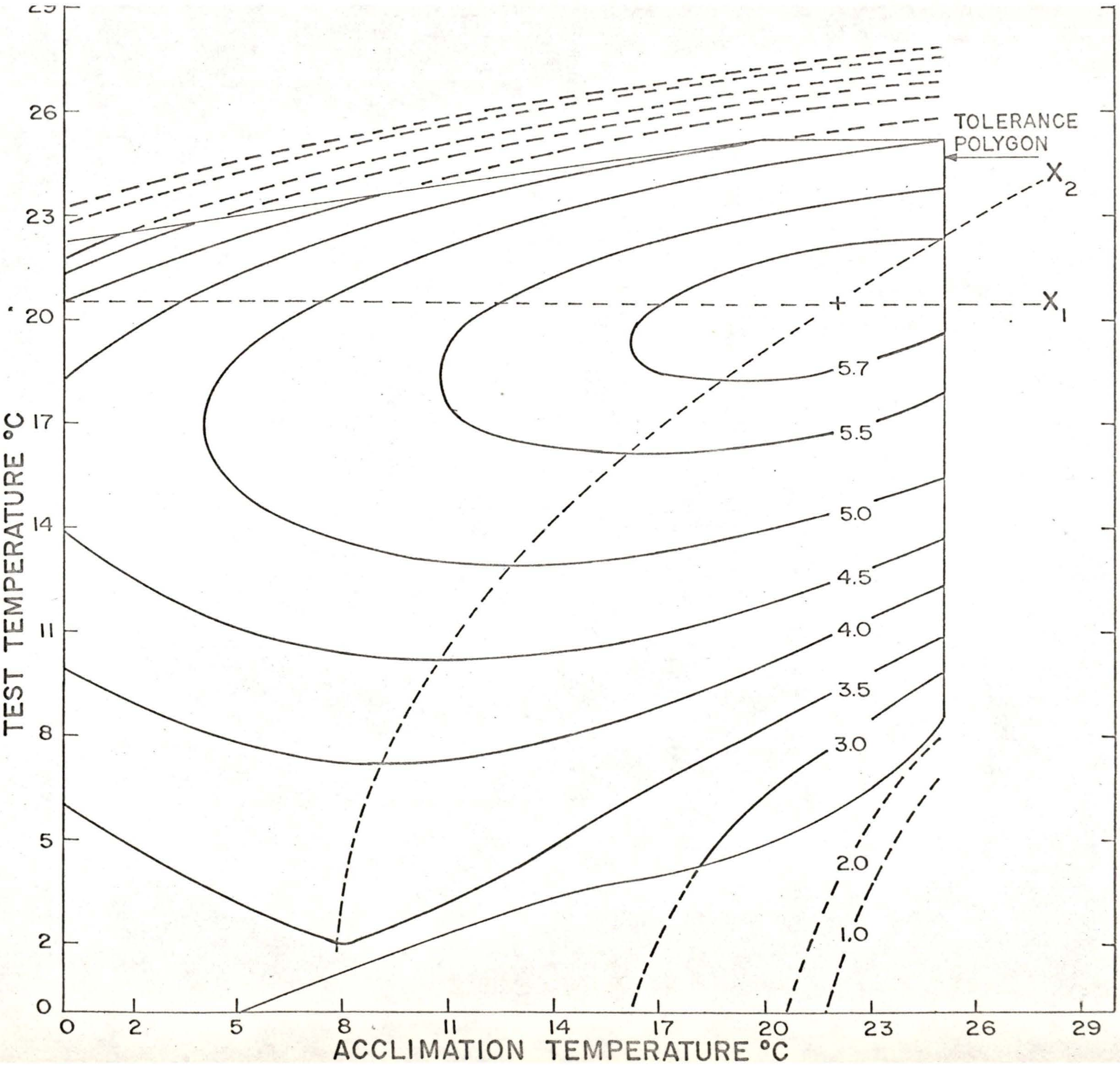
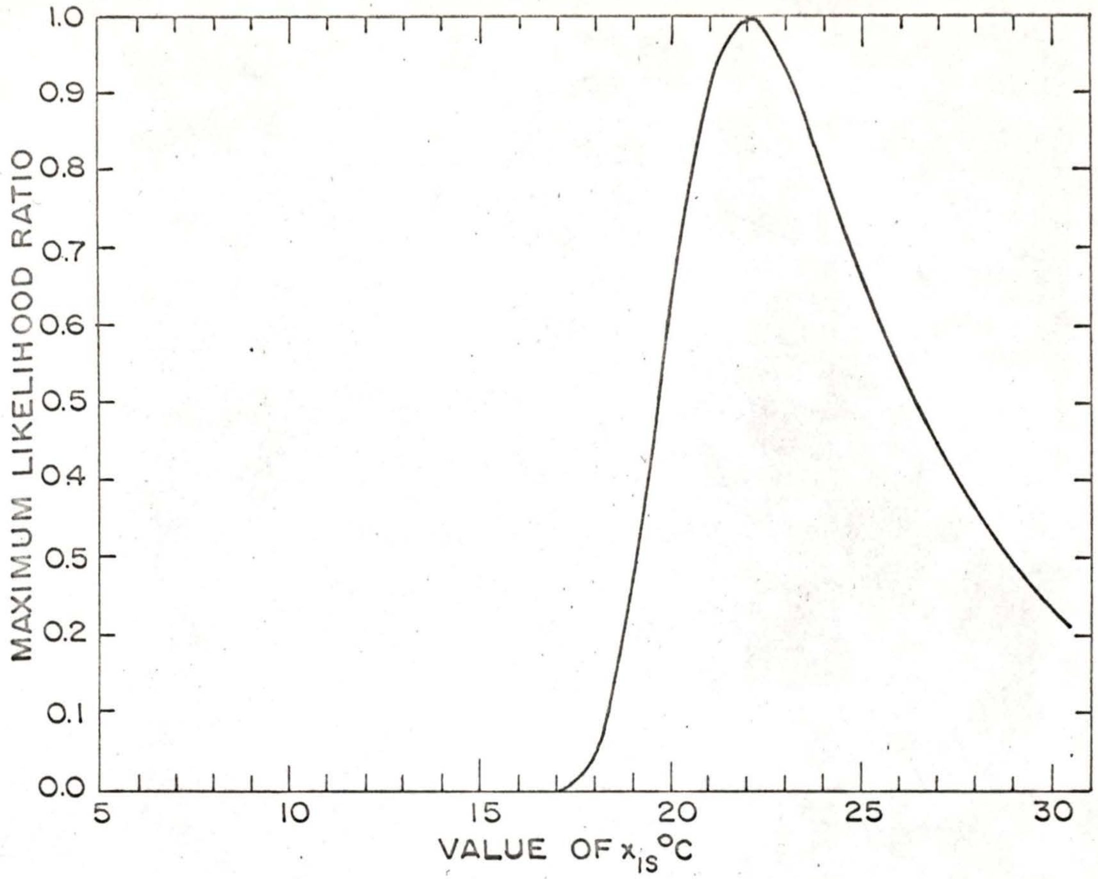
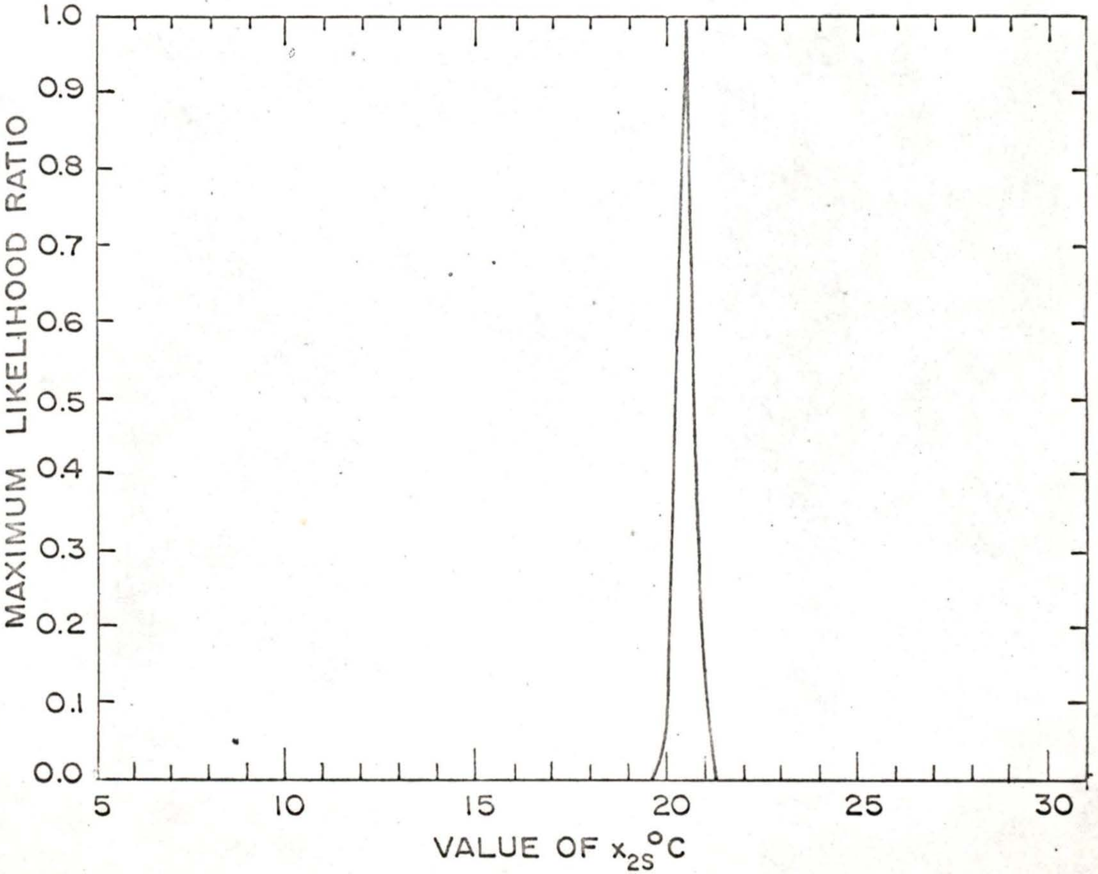

TOLERANCE POLYGON
X₂
X₁
5.7
5.5
5.0
4.5
4.0
3.5
3.0
2.0
1.0
TEST TEMPERATURE °C
0
2
5
8
11
14
17
20
23
26
ACCLIMATION TEMPERATURE °C
0
2
5
8
11
14
17
20
23
26
29

Figure 19

Test series 1, the non-linear model: maximum likelihood ratios of various estimates of the centre coordinates. Upper panel, the acclimation temperature coordinate (x_{1s}). Lower panel, the test temperature coordinate (x_{2s}).



CENTRE AT x_{1S} = 22.035



CENTRE AT x_{2S} = 20.450

The centre of the non-linear model was calculated at:

Acclimation temperature (x_1) = 22.03° C.

test temperature (x_2) = 20.45° C.

The response at the centre was calculated as 5.84 lengths/second. Maximum relative likelihood graphs (Fig. 19) indicate that the acclimation temperature coordinate of the centre was not clearly defined, but the test temperature coordinate was estimated with high precision. The graphs suggest that an acclimation temperature of 20° C and a test temperature of 20° C are plausible estimates of the centre point coordinates.

Coho are able to perform well over most of their tolerance zone (Fig. 18). However, the range of test temperatures over which the coho can maintain a moderate level of performance varies with the acclimation temperature. Fish acclimated to 23° C were able to maintain a swimming speed of at least 3.5 lengths/second over a test temperature range of 15 degrees (10° C - 25° C). Fish acclimated to 8° C were able to maintain at least this level of performance over a 21 degree (2° C - 23° C) range, while those acclimated to 2° C were able to maintain 3.5 lengths/second over only a 17 degree (5° C - 22° C) test temperature range.

The ability of coho to perform, for the test periods employed, outside the tolerance zone, is shown by the dotted lines in Figure 18. The surface suggests that the ability to perform in the lower zone of resistance increases with decreasing acclimation temperatures, although care should be taken not to extrapolate below 2° C, the lower test temperature limit. Conversely, the ability to swim at temperatures in the upper zone of resistance appears greatest for warm acclimated fish.

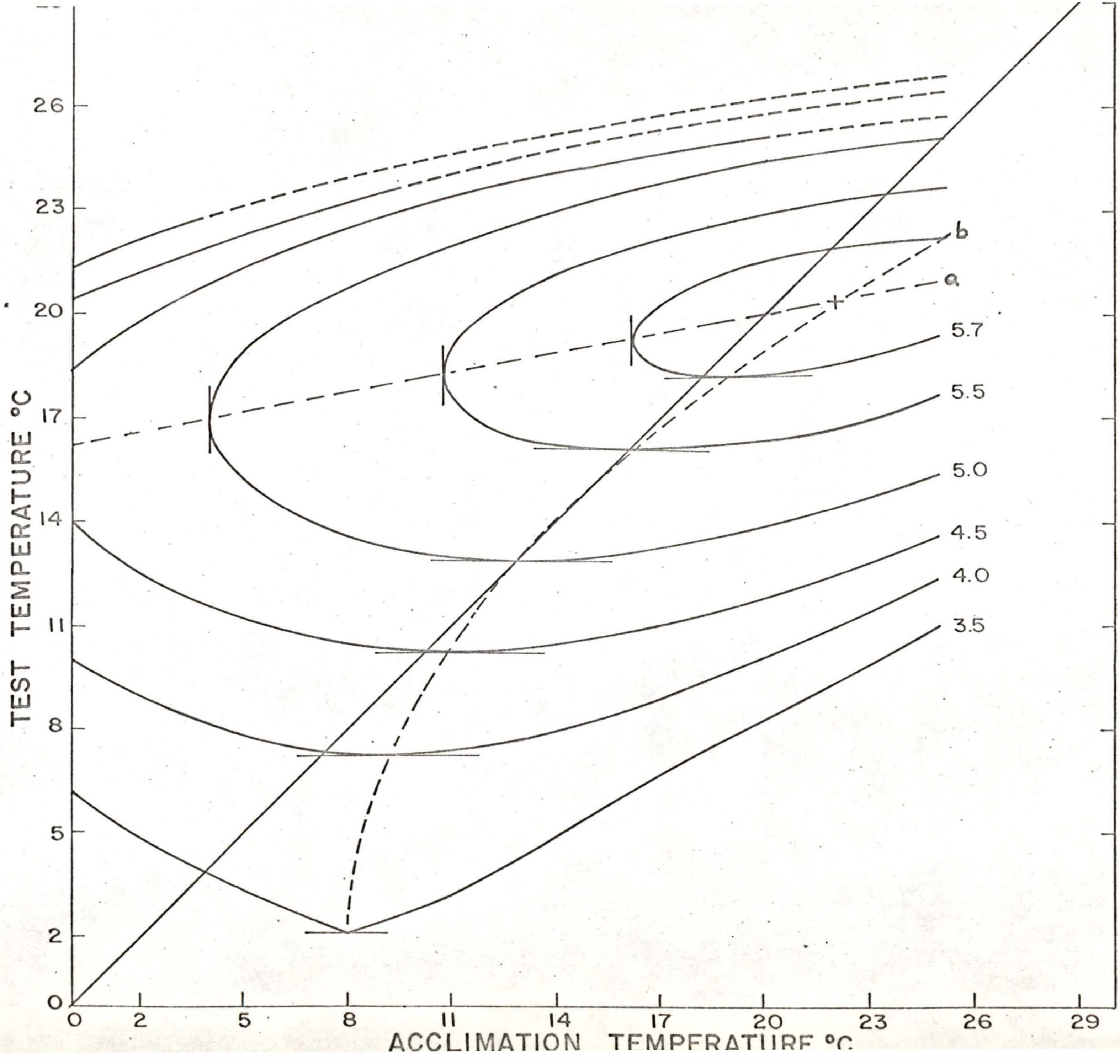
The axes of the non-linear response surface are denoted by X_1 and X_2. While these axes would be linear and orthogonal when considered in terms of the transformed data (x^{α} coordinates), they are neither linear nor orthogonal when recalculated in the original units of measurement (x coordinates) as shown in Fig. 18. The biological significance of the X-axes is not entirely obvious. However, the X_2-axis (Fig. 18) appears to define the axis of maximum performance with respect to acclimation temperature for given test temperatures.

A knowledge of the test temperatures at which coho perform best for a given acclimation temperature is important in evaluating the shape of the response surface. An axis denoting the test temperature of maximal response for each acclimation temperature was determined by constructing vertical tangents to the response isopleths (Fig. 20). This axis (a) defined the position of a ridge of maximal performance in relation to test temperature for given acclimation temperatures. Conditions of equal acclimation and test temperature are shown by the diagonal construction line in the figure. Comparison of the diagonal with the axis of the ridge indicates that maximal performance of coho acclimated to 2° C occurred at a test temperature 16.6° C. The discrepancy between the acclimation temperature and the temperature which provides maximal performance decreases until the two temperatures coincide near the centre of the surface, at about 20° C.

The second axis (b) of Fig. 20 defines the acclimation temperature producing maximal performance at a given test temperature and is apparently identical to the X_2-axis of Fig. 18. The curvature of this axis suggests that the fish performing best at a given test temperature may not be those acclimated to that temperature.

Figure 20

Axes of maximal performance for test series 1. Axis a defines the test temperature producing maximal performance at each acclimation temperature. Axis b defines the acclimation temperature producing maximal performance at each test temperature. The diagonal construction line indicates conditions of equal acclimation and test temperatures.


TEST TEMPERATURE °C
0
2
5
8
11
14
17
20
23
26
ACCLIMATION TEMPERATURE °C
0
2
5
8
11
14
17
20
23
26
29
b
a
5.7
5.5
5.0
4.5
4.0
3.5

Test Series 2 (January 30, 1969 to April 11, 1969)

Data for the second test series (Appendix II) was used to calculate, on the basis of the linear model, the second degree polynomial

$$Y = 1.534 + 0.058x_1 + 0.429x_2 - 0.006x_1^2 - 0.016x_2^2 + 0.007x_1x_2$$

Analysis of variance (Table IX) indicated that only the term for the linear effect of acclimation temperature (x_1) could be removed from the polynomial without affecting the adequacy of the model.

Examination of the canonical equation

$$Y - 5.518 = -0.1740X_1^2 - 0.0049X_2^2$$

indicated that the surface contained a true maximum. The centre of the response surface was calculated at:

acclimation temperature (x_1) = 14.77°C.

test temperature (x_2) = 16.57°C.

Again, the x_2 coordinate of the centre point was estimated precisely, but the x_1 coordinate was not clearly defined (Fig. 21). The calculated swimming speed at the centre was 5.52 lengths/second.

The plot of the linear surface (Fig. 22) is very similar to the linear surface fitted to the series 1 data. However, the centre of the series 2 surface occurred at slightly higher acclimation and test temperatures, suggesting a translocation of the response surface in the factor space. A change in the degree of rotation of the surface with regard to the axes of measurement is not apparent. However, the comparison indicates that differences in capacity do exist, as fish in the second series were able to perform at higher velocities than those in the first series.

The power parameters of the non-linear model fitted to test

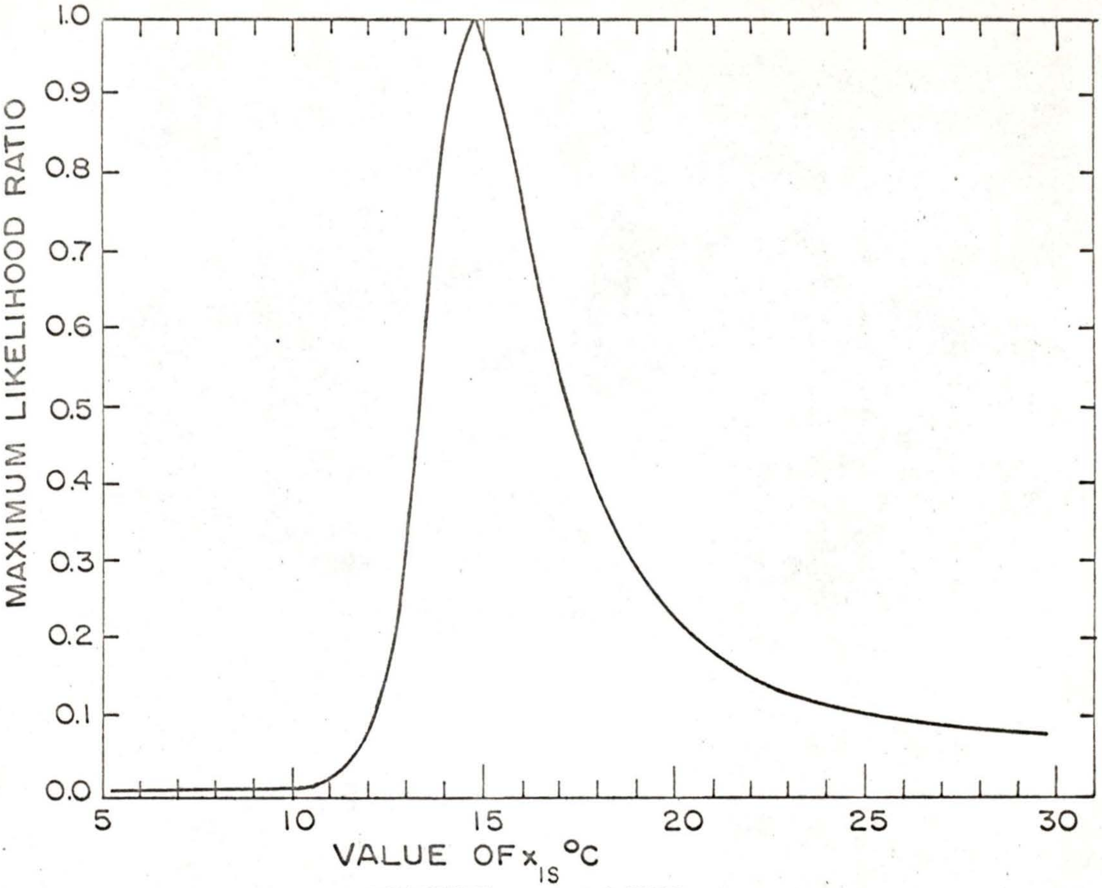
Table IX. Analysis of variance of the untransformed data from test series 2.

Source of Variation	SS	d.f.	MSS	F
Treatments	84.70	63	1.34	2.98 **
Linear	24.21	2	12.10	26.85 **
x_1 linear	0.01	1	0.01	0.03
x_2 linear	23.03	1	23.03	51.09 **
Quadratic	32.79	2	16.39	36.37 **
x_1 Quad.	3.72	1	3.72	8.25 **
x_2 Quad.	31.06	1	31.06	68.90 **
$x_1 * x_2$	6.02	1	6.02	13.35 **
Lack of fit	26.14	58	0.45	
Total	84.70	63		

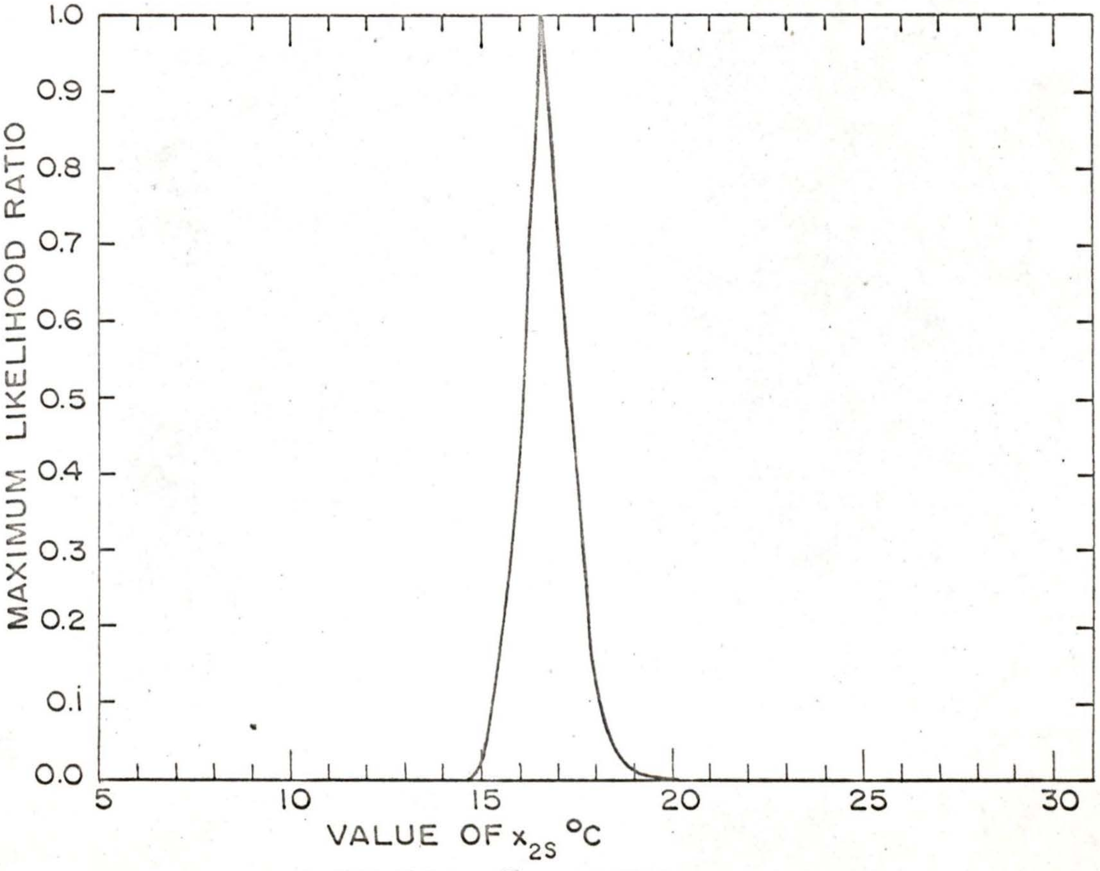
* P = 0.05
** P = 0.01

Figure 21

Test series 2; the linear model. Maximum likelihood ratios for various estimates of the centre coordinates. The acclimation temperature coordinate (x_{1s}) is shown in the upper panel; the test temperature coordinate (x_{2s}) in the lower.



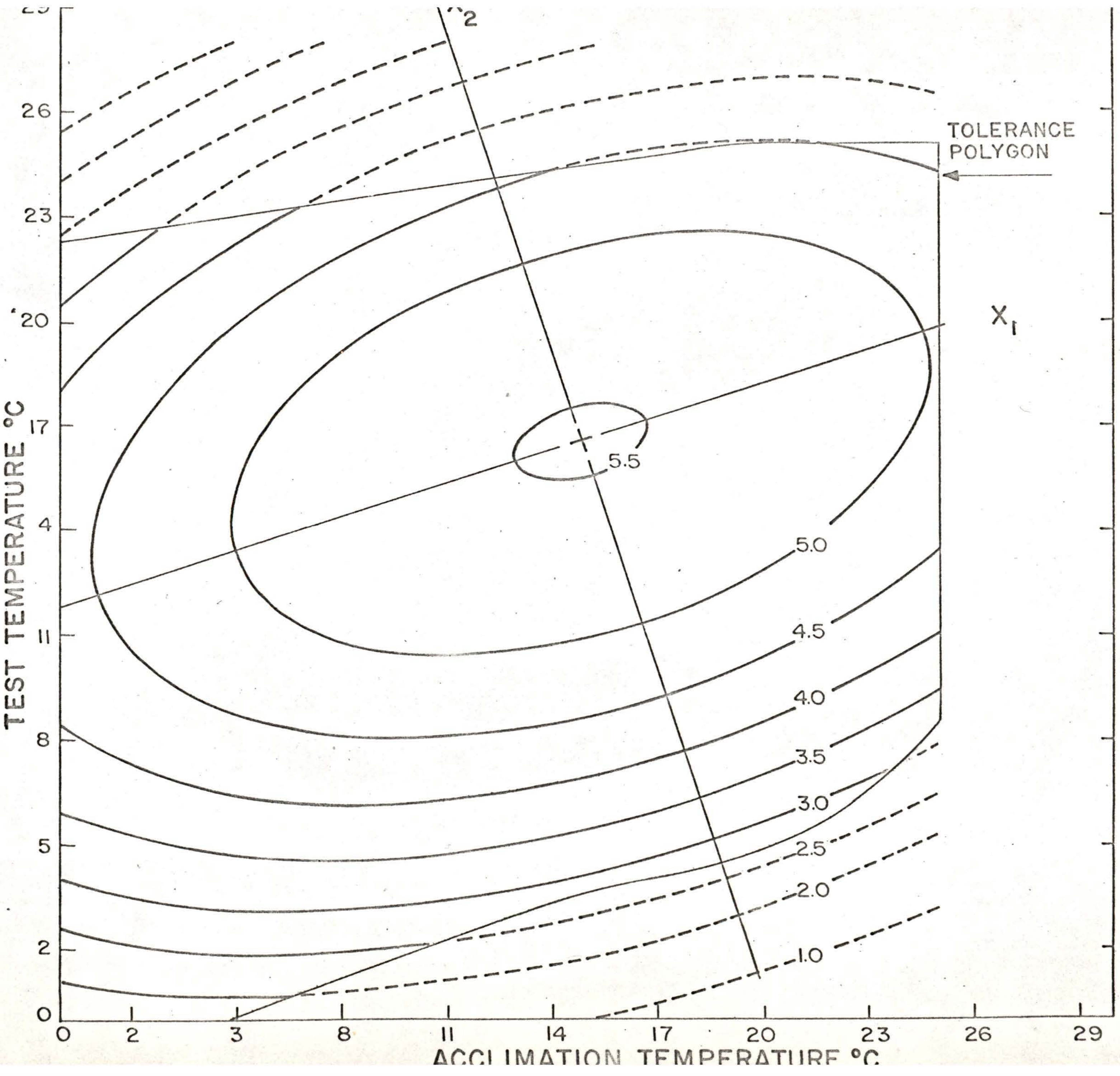
CENTRE $x_{1S} = 14.774$



CENTRE AT $x_{2S} = 16.570$

Figure 22

The linear response surface fitted to the data from test series 2. The isopleths are swimming speeds in lengths/second and are dotted outside the tolerance polygon.


X2
TOLERANCE POLYGON
X1
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.0
TEST TEMPERATURE °C
0
2
5
8
11
4
17
20
23
26
ACCLIMATION TEMPERATURE °C
0
2
3
8
11
14
17
20
23
26
29

series 2 were:

$$\alpha_1 = 0.564$$
$$\alpha_2 = 2.177$$
$$\gamma = 2.476$$

The parameter α_2 was somewhat more precisely estimated than the others (Figs. 23, 24 and 25).

The non-linear polynomial was calculated as

$$Y^{2.48} = 2.065 + 12.252x_1^{0.56} + 0.121x_2^{2.18} - 2.213x_1^{1.12} - 0.00016x_2^{4.36} + 0.018x_1^{0.56}x_2^{2.18} .$$

Analysis of variance (Table X) indicated that none of the terms could be removed without appreciably affecting the adequacy of the model.

The relative likelihood of the linear model versus the non-linear model (2.99×10^{-10}) suggested that the non-linear model provided a superior fit for the observed data.

The canonical equation

$$Y - 75.370 = -2.213X_1^2 - 0.00013X_2^2$$

was used for plotting the response surface (Fig. 27). The centre was calculated at:

acclimation temperature (x_1) = 20.15° C

test temperature (x_2) = 19.71° C.

The calculated swimming speed at the centre was 5.73 lengths/second. the maximum likelihood plots of the centre point (Fig. 26) indicate that the x_2-coordinate of the centre was estimated with extremely high precision, but the x_1-coordinate was poorly defined. The likelihood of both centre coordinates being 20°C was high.

Figure 23

Test series 2. Maximum likelihood ratios for various estimates of the power parameter α_1.

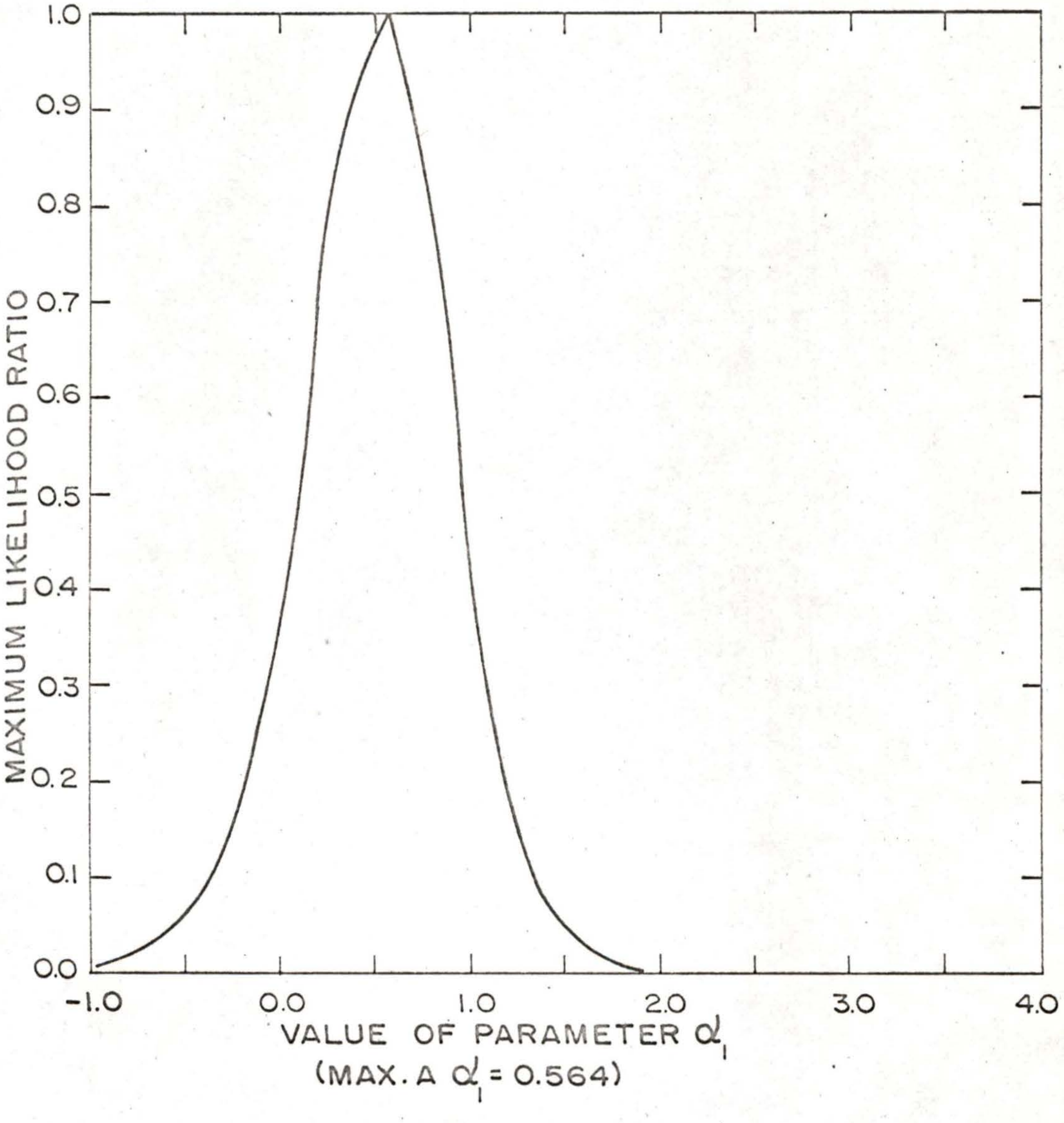

MAXIMUM LIKELIHOOD RATIO
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-1.0
0.0
1.0
2.0
3.0
4.0
VALUE OF PARAMETER α_1
(MAX. A α_1 = 0.564)

Figure 24

Test series 2. Maximum likelihood ratios for various estimates of the power parameter α_2.

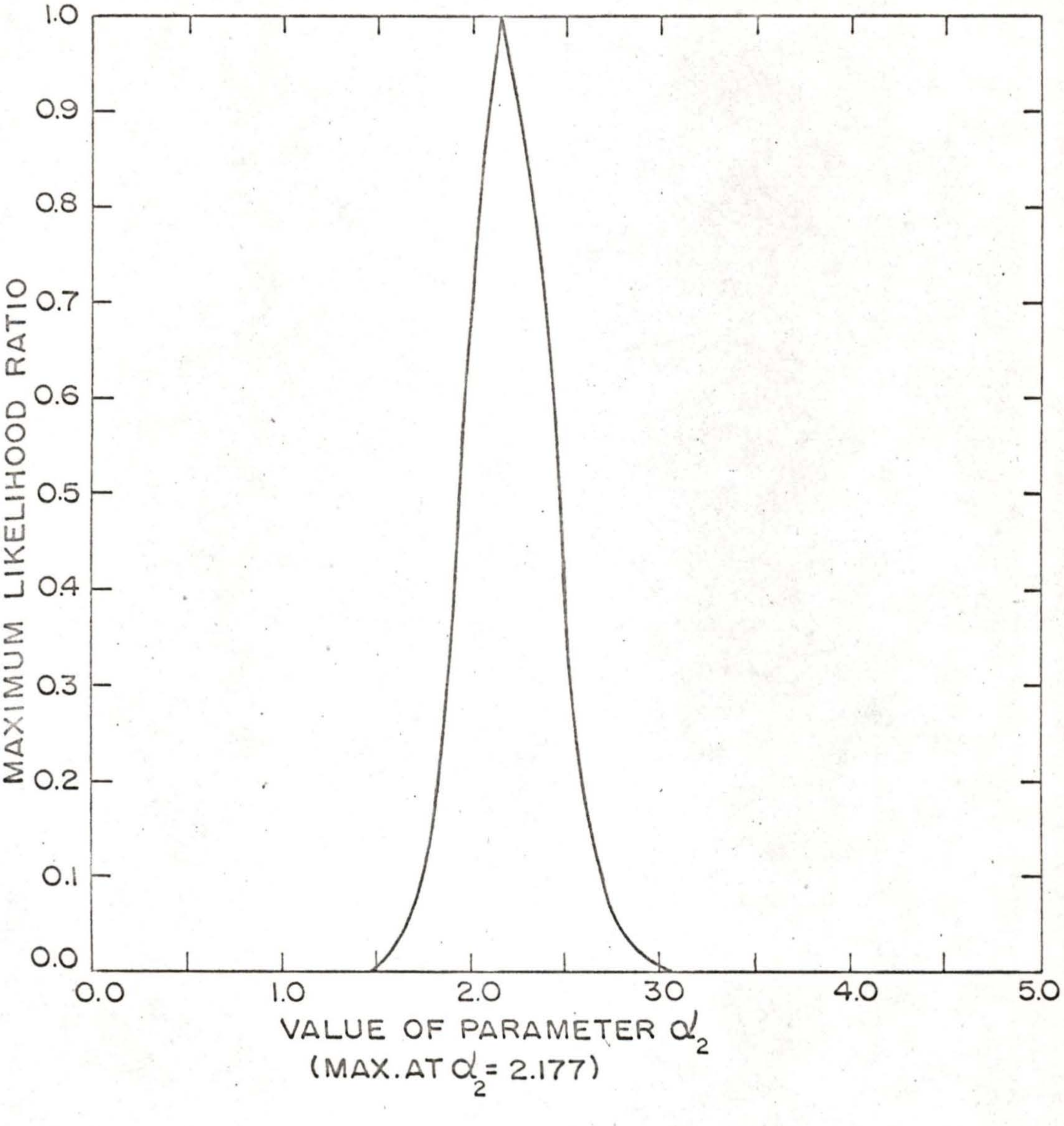

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
MAXIMUM LIKELIHOOD RATIO
0.0
1.0
2.0
3.0
4.0
5.0
VALUE OF PARAMETER α_2
(MAX. AT α_2 = 2.177)

Figure 25

Test series 2. Maximum likelihood ratios for various estimates of the power parameter γ.

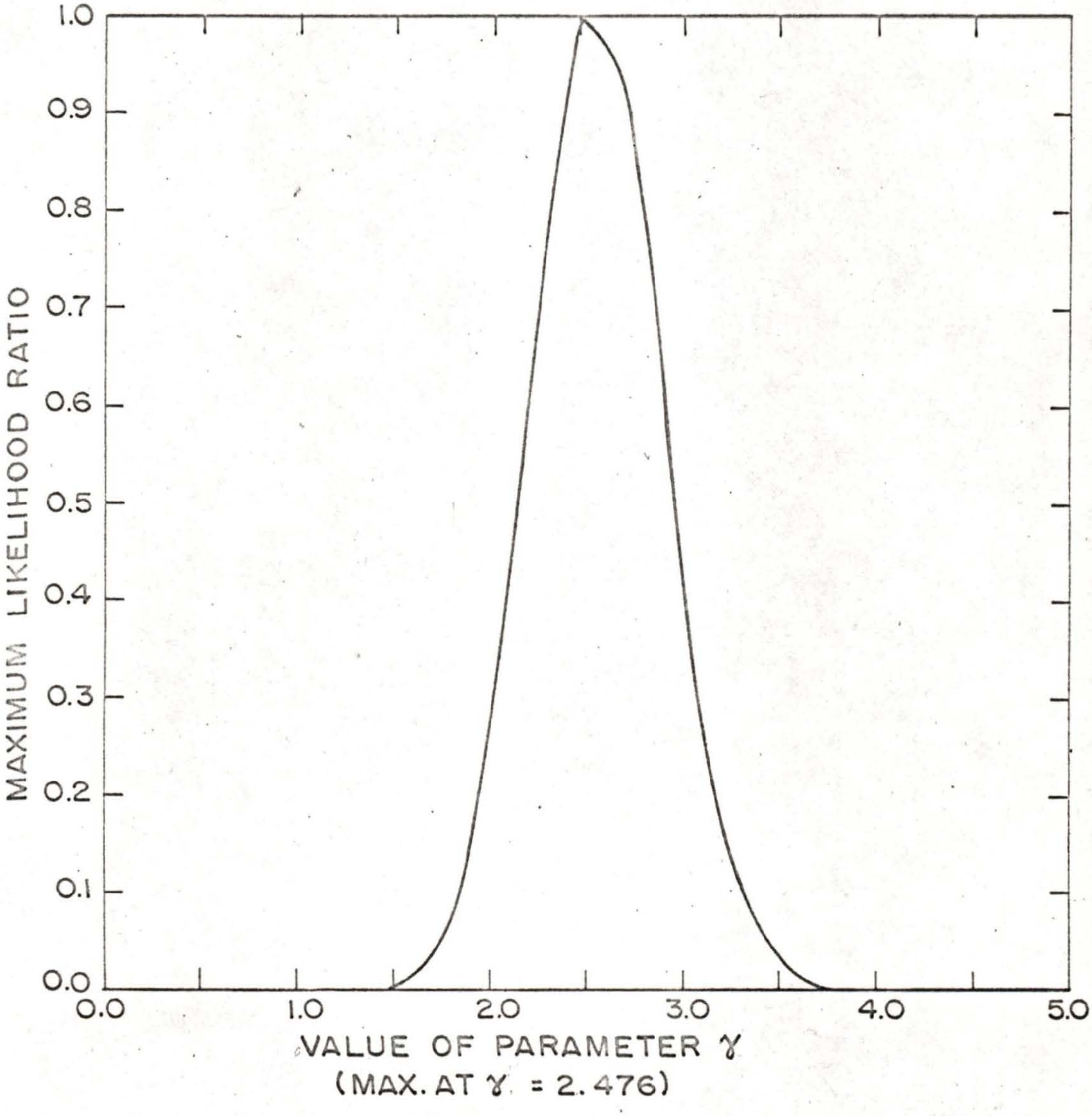
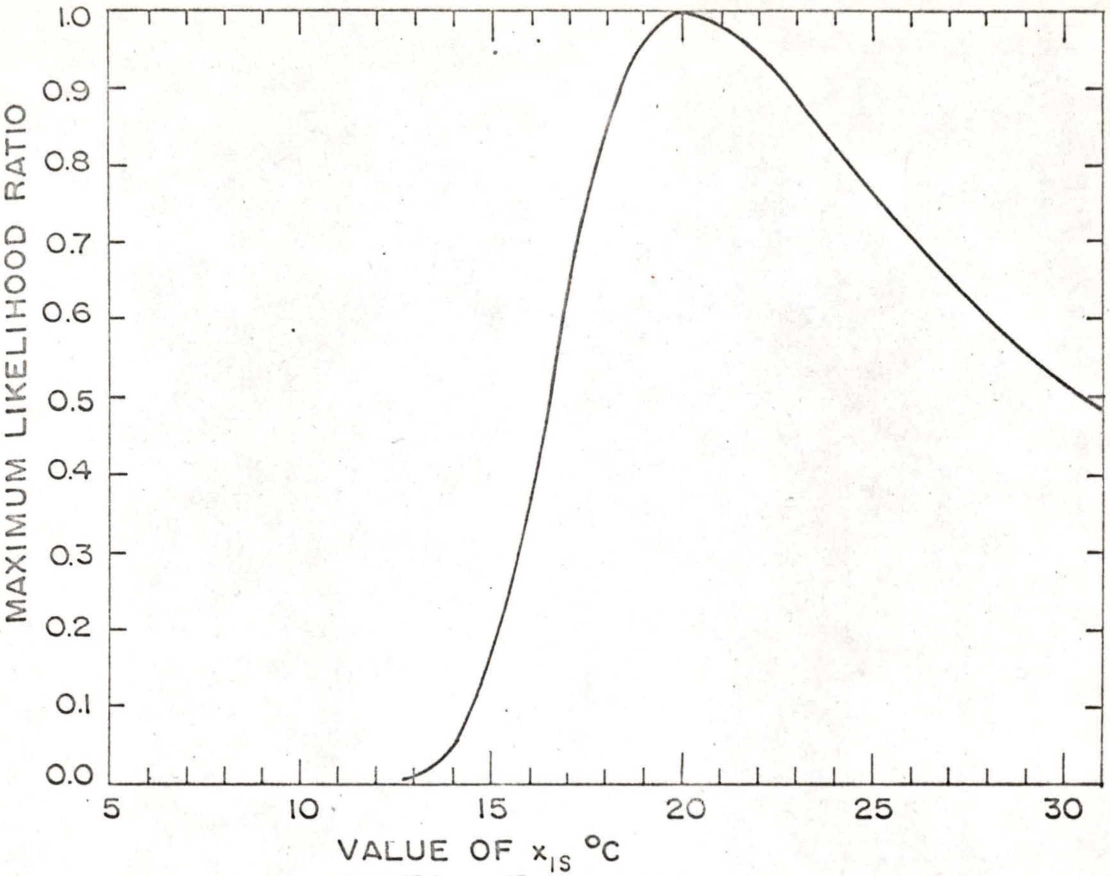
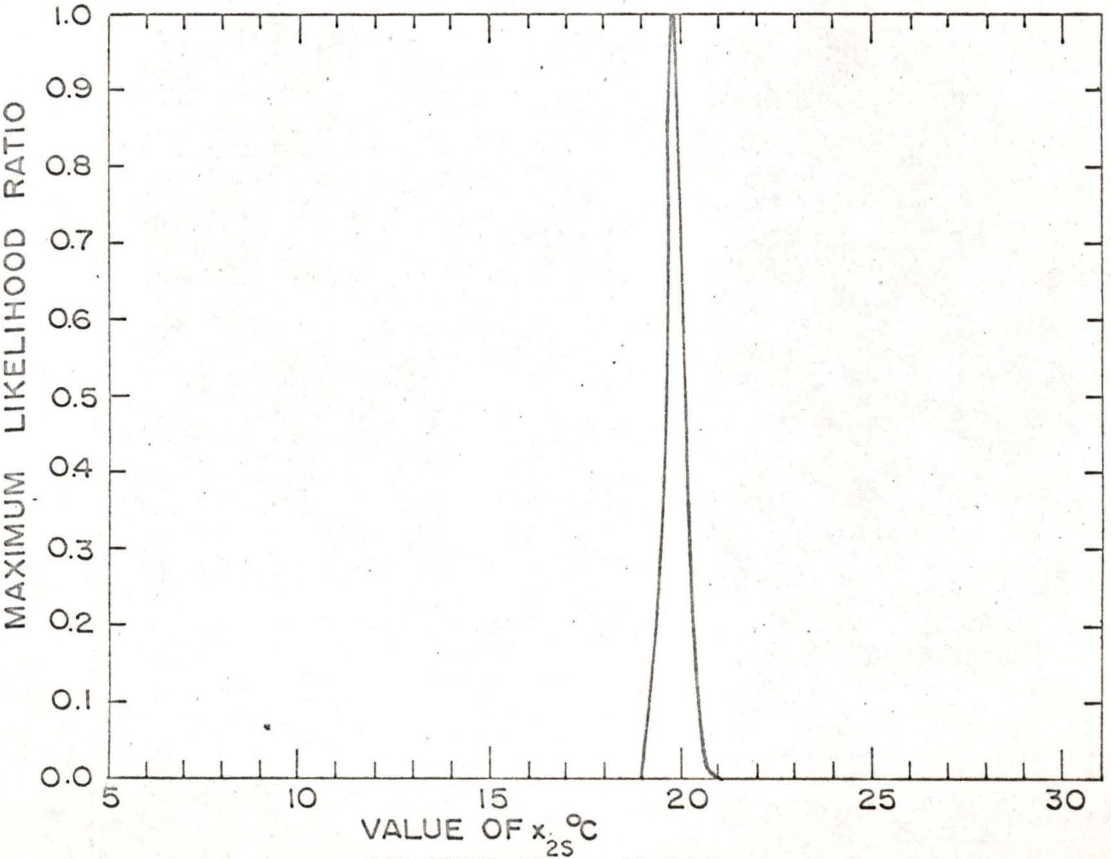

MAXIMUM LIKELIHOOD RATIO
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
1.0
2.0
3.0
4.0
5.0
VALUE OF PARAMETER γ
(MAX. AT γ = 2.476)

Figure 26

Test series 2. Maximum likelihood ratios for the centre coordinates of the non-linear model. The acclimation temperature coordinate (x_{1s}) is shown in the upper panel; the test temperature coordinate (x_{2s}) is below.



CENTRE AT $x_{1S} = 20.153$



CENTRE AT $x_{2S} = 19.705$

Figure 27

The non-linear response surface fitted to the data from test series 2. Isopleths of swimming speed (lengths/second) are dotted outside the tolerance polygon. The axes of the response surface are denoted by X_1 and X_2.

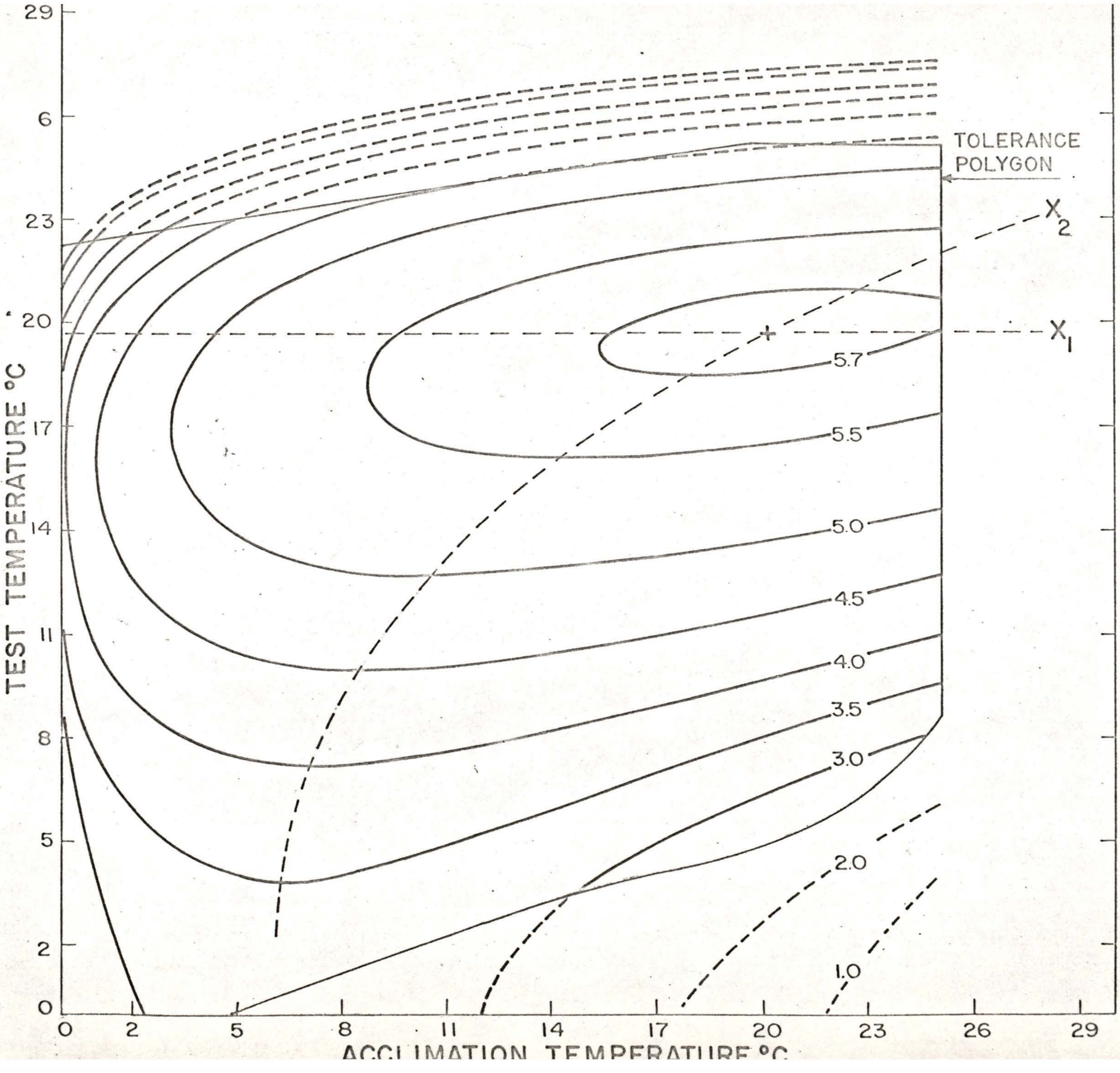

TOLERANCE POLYGON
X_2
X_1
5.7
5.5
5.0
4.5
4.0
3.5
3.0
2.0
1.0
TEST TEMPERATURE °C
29
6
23
20
17
14
11
8
5
2
0
0
2
5
8
11
14
17
20
23
26
29
ACCLIMATION TEMPERATURE °C

Table X. Analysis of variance of the transformed data from test series 2.

Source of Variation	SS	d.f.	MSS	Approx. F	MIR
Treatments	76.65	63	1.21	5.07	2.10×10^{-27}
Linear	11.71	2	5.85	24.45	1.44×10^{-9}
x_1 linear	1.76	1	1.76	7.37	1.78×10^{-2}
x_2 linear	7.47	1	7.47	31.19	5.71×10^{-7}
Quadratic	46.67	2	23.33	97.42	9.25×10^{-22}
x_1 Quad.	2.28	1	2.28	9.54	5.98×10^{-3}
x_2 Quad.	45.58	1	45.58	190.30	1.66×10^{-21}
$x_1 * x_2$	7.34	1	7.34	30.67	6.91×10^{-7}
Transform	12.97	3	4.32	18.04	2.99×10^{-10}
Lack of fit	13.17	55	0.23		
Total	76.65	63			

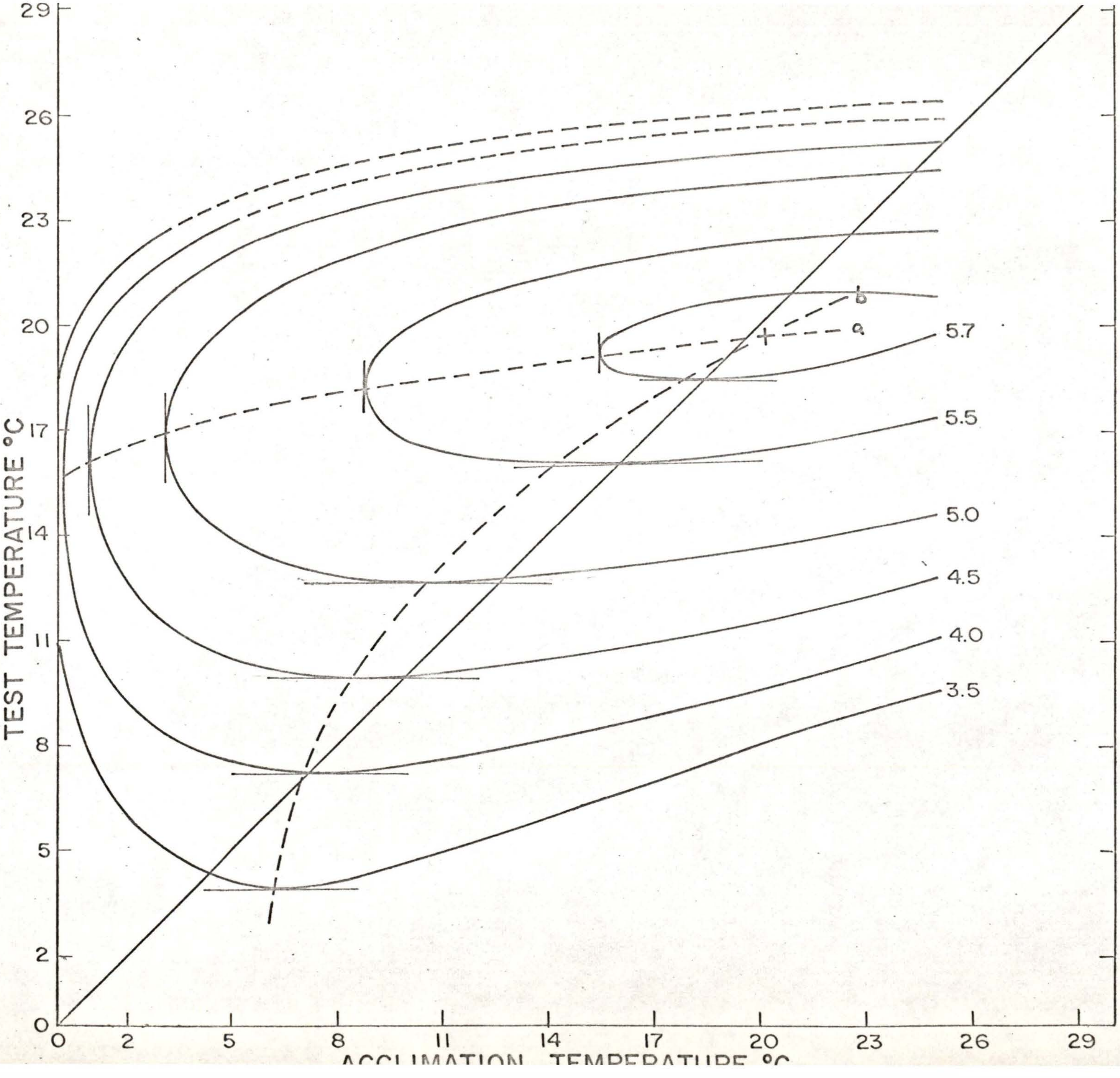
The non-linear response surface fitted to the data of test series 2 (Fig. 27) was basically similar to the non-linear surface for the first series. The coho demonstrated a high capability to perform over most of the tolerance zone. However, the range of test temperatures over which at least a moderate swimming speed could be maintained varied with the acclimation temperature. A level of 3.5 lengths/second was maintained over a 16 degree range (9° C - 25° C) by 23° C acclimated fish. Coho acclimated to 8° C maintained at least this level of performance over a 19 degree temperature range (4° C - 23° C), while 2° C acclimated coho could maintain 3.5 lengths/second over only a 16 degree range (6° C - 22° C).

Performance of coho in the second series at temperatures near the boundaries of the tolerance domain differed slightly from the performance of those in series 1. When acclimated to temperatures between 5° C and 17° C, fish of the second series were able to maintain higher swimming speeds in the upper portion of the resistance zone than those in series 1. However, when these two groups were acclimated to temperatures above 17° C., their performance in the upper resistance zone was almost identical. At acclimation temperatures other than above 20° C., the swimming speeds of the series 2 fish at test temperatures near the lower lethal limits were slightly slower than the speeds attained by the series 1 fish. The performance of 2° C. acclimated fish was lower at all test temperatures in test series 2.

The axes of maximum response for a given acclimation or test temperature (Fig. 28) were similar to those determined for series 1. For given acclimation temperatures, the test temperatures producing maximum response defined a rising ridge (axis a) which

Figure 28

Axes of maximum response for test series 2. The test temperatures producing maximum response at each acclimation temperature is defined by axis (a); the acclimation temperature producing maximum response at each test temperature is defined by axis (b). The diagonal construction line indicates conditions of equal acclimation and test temperatures.


TEST TEMPERATURE °C
29
26
23
20
17
14
11
8
5
2
0
0
2
5
8
11
14
17
20
23
26
29
ACCLIMATION TEMPERATURE °C
5.7
5.5
5.0
4.5
4.0
3.5
b
a

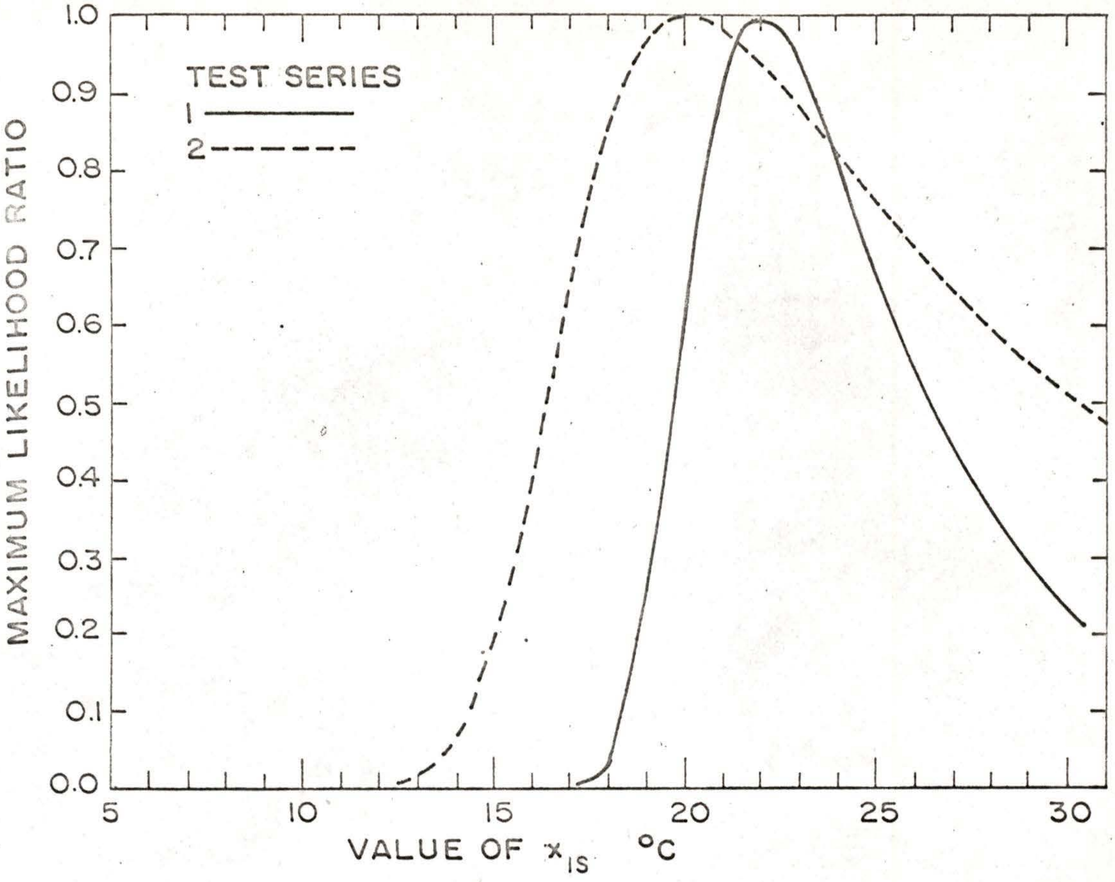
began at 16.5° C. for 2° C. acclimated fish and crossed the equal acclimation temperature-test temperature diagonal at 19.6° C. The curvilinearity of the ridge suggests that the interaction of test and acclimation temperatures was not constant at all levels of acclimation. The second axis (b) of the figure defined the acclimation temperatures producing maximal performance at given test temperatures. Again, this axis suggested that the fish performing best at a given temperature may not be those acclimated to that temperature. Comparison with the first test series suggests a translation of the second series axis such that the acclimation temperatures producing maximal performance at each test temperature were slightly lower in series 2.

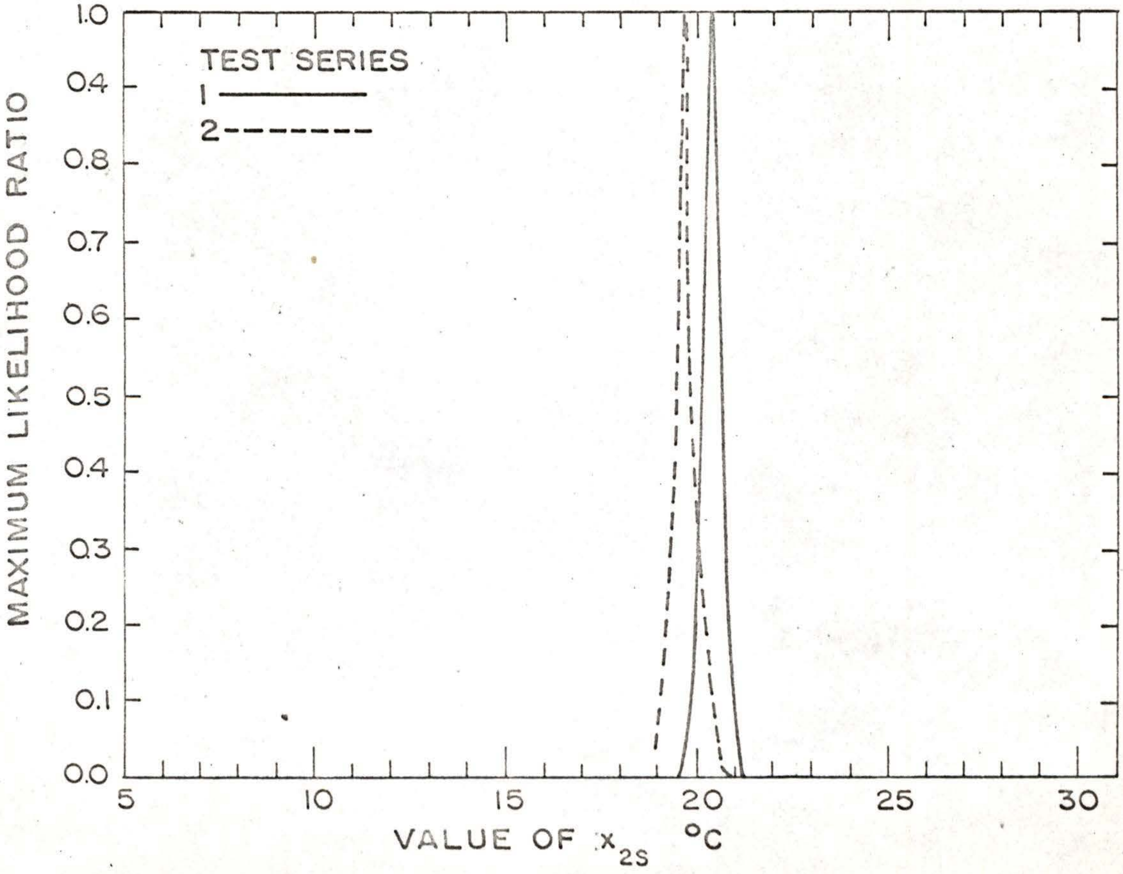
The non-linear response surfaces fitted to test series 1 and 2 were generally similar, but not identical. Translation of the surface (movement with respect to the axes of measurement) and a change in capacity (swimming speed at the surface centre) were apparent from comparison of the linear surfaces. The differences in the non-linear surfaces appeared more complex. The changes in these surfaces could not be explained by rotation or translation of the whole surface, and capacity differences at the centres were quite small. A change in the shape and spacing of the isopleths appeared to be involved rather than in integral movement of the whole surface. This may be described as an inner rotation of the response surface (Alderdice, MS).

Differences occurring between the two non-linear response surfaces of series 1 and 2 were examined from relative likelihood plots. The plots of the centre coordinates (Fig. 29) indicated that an acclimation temperature of 20° C. and a test temperature of 20° C. were

Figure 29

Comparison of the centre coordinates of the non-linear response surfaces for test series 1 and 2. The acclimation temperature coordinates (x_{1s}) are shown in the upper panel; the test temperature coordinates (x_{2s}) in the lower.


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
MAXIMUM LIKELIHOOD RATIO
TEST SERIES
1
2
5
10
15
20
25
30
VALUE OF x_{1S} °C


1.0
0.4
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
MAXIMUM LIKELIHOOD RATIO
TEST SERIES
1
2
5
10
15
20
25
30
VALUE OF x_{2S} °C

plausible estimates for the centres of both surfaces. Common estimates could also be determined for the power parameters (α_1, α_2, and γ ; Figs. 30, 31 and 32) which would have a high relative likelihood for each test series. The maximum likelihood estimates of the power parameters calculated for test series 1 were plausible, but near borderline estimates for the corresponding parameters in test series 2 $R(\alpha_1 = 1.16, \alpha_2 = 2.35, \gamma = 2.37) = 0.12$. Conversely, the maximum likelihood estimates of the power parameters for series 2 were unlikely estimates of the series 1 power parameters $R(\alpha_1 = 0.564, \alpha_2 = 2.18, \gamma = 2.48) = 0.04$. While there were basic similarities in the non-linear response surfaces, the differences were great enough that little would be gained by combining the data of the two test series. It is interesting to note, however, that a best combined estimate of the centre of the capacity surface may be gained by noting the temperatures (Fig. 29) at which the maximum likelihood ratios are highest (intersection) for both test series. On this basis the centre of the non-linear surface is estimated at an acclimation temperature of about 21.5° C and a test temperature of slightly greater than 20.0° C.

Test Series 3 (April 14, 1969 to April 25, 1969).

Test series 3 was designed to determine the effects of acclimation temperature (x_1), test temperature (x_2) and size (x_3) on swimming speeds (Appendix III). For the linear model, the second degree polynomial was:

$$Y = 2.160 + 0.091x_1 + 0.195x_2 + 1.362x_3 - 0.110x_1^2 - 0.014x_2^2 - 0.089x_3^2 + 0.015x_1x_2 + 0.007x_1x_3 + 0.004x_2x_3.$$

Figure 30

Comparison of the power parameter α_1 for test series 1 and 2.

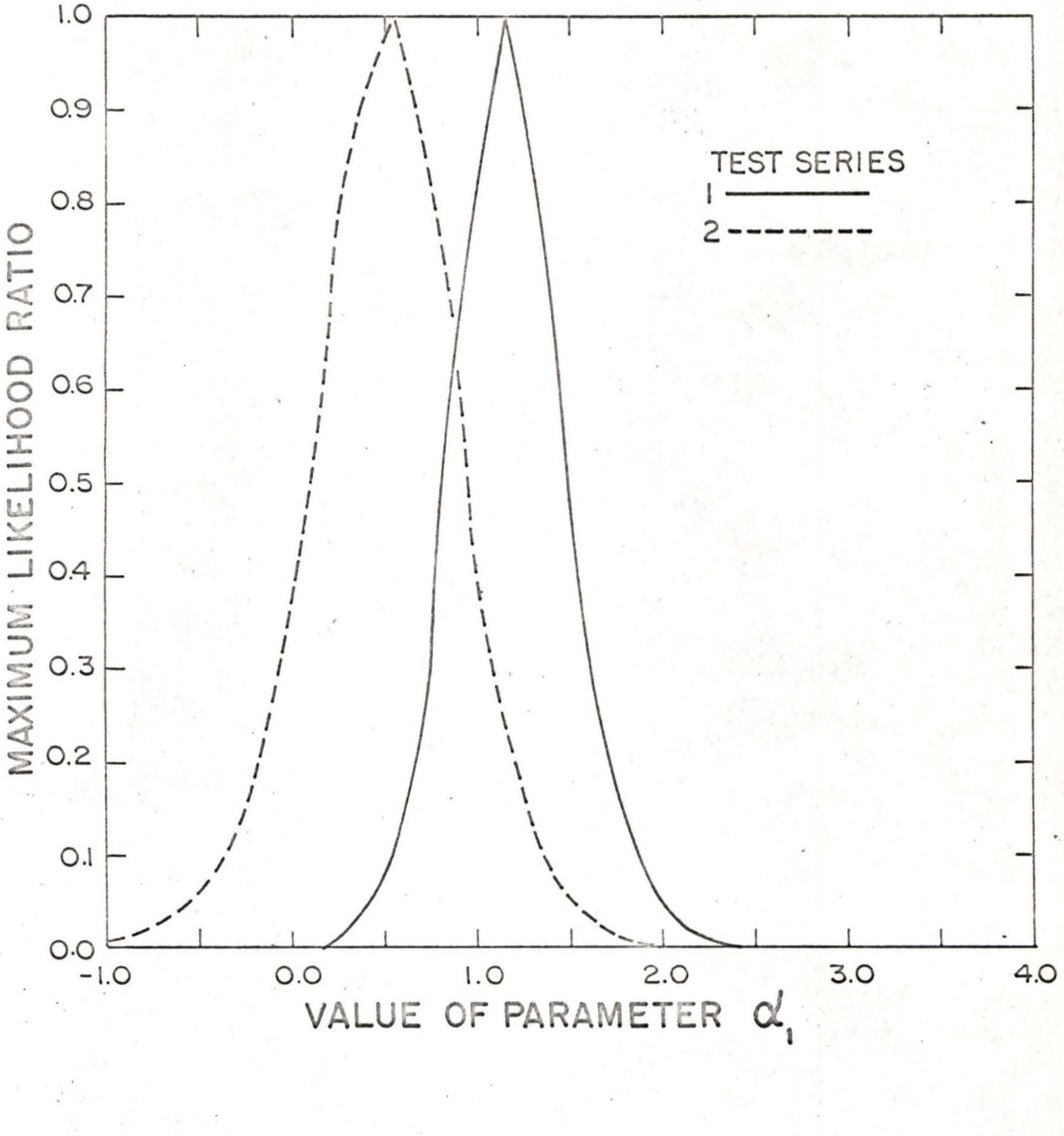

MAXIMUM LIKELIHOOD RATIO
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-1.0
0.0
1.0
2.0
3.0
4.0
VALUE OF PARAMETER α_1
TEST SERIES
1
2

Figure 31

Comparison of the power parameter α_2 for test series 1 and 2.

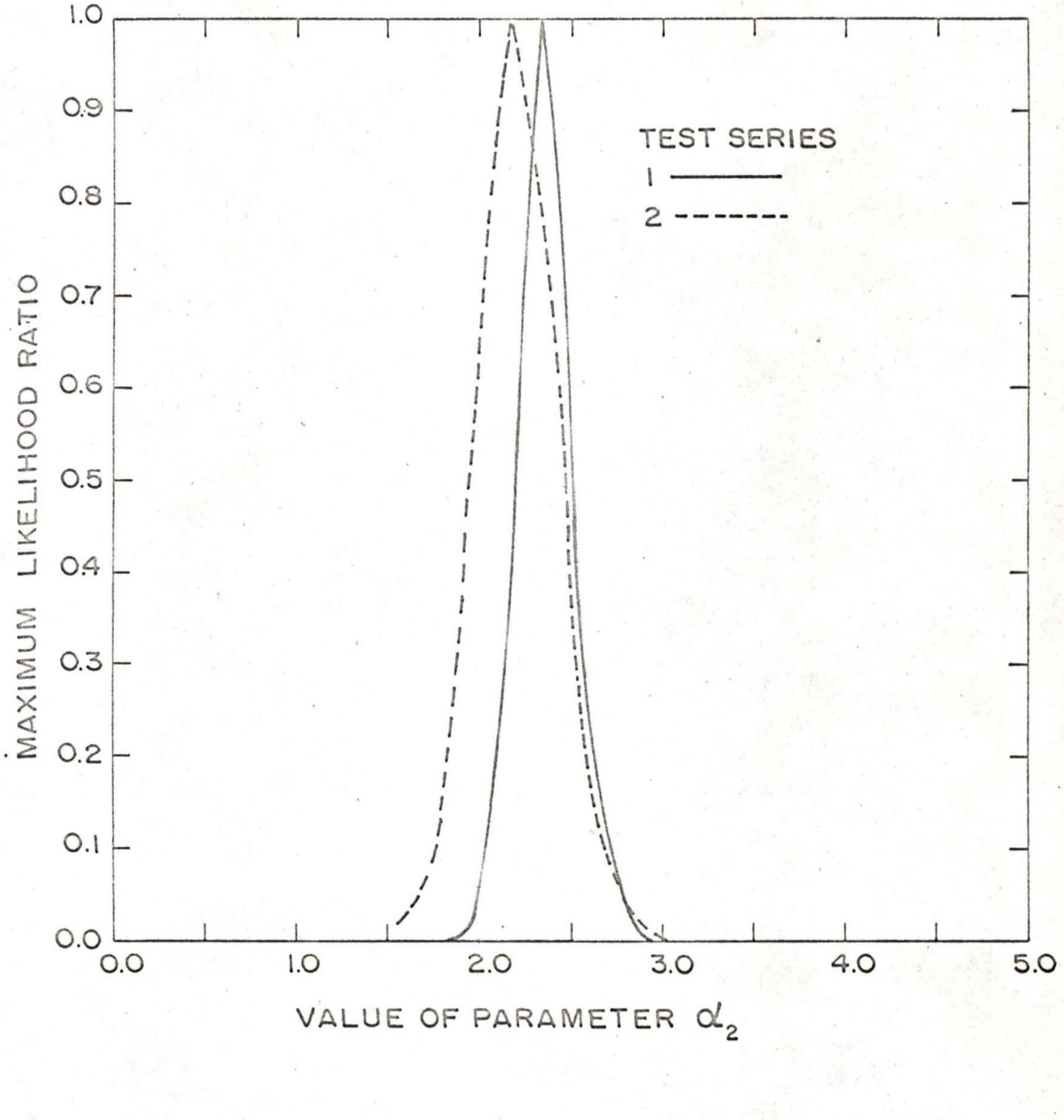
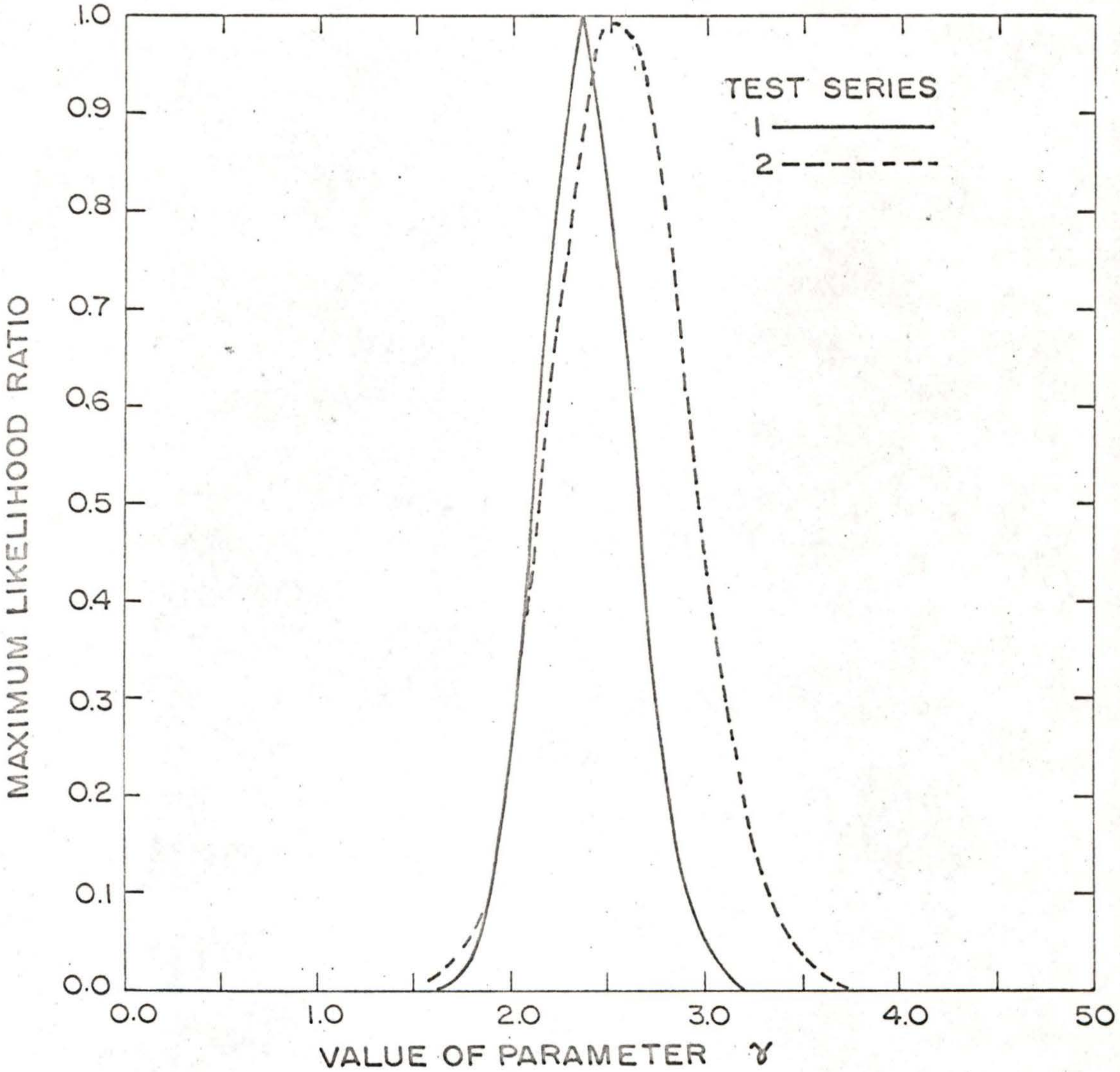

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
MAXIMUM LIKELIHOOD RATIO
TEST SERIES
1
2
0.0
1.0
2.0
3.0
4.0
5.0
VALUE OF PARAMETER α_2

Figure 32

Comparison of the power parameter γ for test series 1 and 2.


MAXIMUM LIKELIHOOD RATIO
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
1.0
2.0
3.0
4.0
50
VALUE OF PARAMETER γ
TEST SERIES
1 ———
2 - - - - -

Analysis of variance (Table XI) indicated that the terms associated with the linear and quadratic effects of size (x_3), the interactions of size with acclimation temperature ($x_1 * x_3$) and test temperature ($x_2 * x_3$), and the linear effect of test temperature (x_2) could all be removed without greatly affecting the adequacy of the model.

The linear model in this series of experiments does not allow one to measure the relationship between size, temperature and swimming speed. Hence, further analysis of the data with respect to the linear model was set aside in favour of analysis employing the non-linear model.

The power parameters of the non-linear model fitted to the third series were:

$\alpha_1 = -1.89$

$\alpha_2 = 4.69$

$\alpha_3 = 0.140$

$\gamma = 1.000$

None of these parameters were precisely estimated (Figs. 33, 34, 35 and 36). The likelihood plot of α_3 indicated that the effect of size was poorly defined.

The non-linear polynomial

$$Y^{1.0} = 293.8 + 321.8x_1^{-1.89} + 4.94 \times 10^{-6} x_2^{4.69} + 440.1x_3^{0.14} - 3725.0x_1^{-3.78} - 2.68 \times 10^{-12} x_2^{9.38} - 163.4x_3^{0.28} - 4.26 \times 10^{-5} x_1^{1.89} x_2^{4.69} - 83.90x_1^{-1.89} x_3^{0.14}$$

was calculated. Analysis of variance (Table XII) indicated that the linear effect of test temperature (x_2) and the interactions of size with acclimation temperature ($x_1 * x_3$) and test temperature ($x_2 * x_3$)

Table XI. Analysis of variance of the untransformed data for test series 3.

Source of Variation	SS	d.f.	MSS	F
Treatments	43.07	26	1.65	3.21 **
Linear	4.38	3	1.46	2.83
x_1 linear	2.47	1	2.47	4.80 *
x_2 linear	1.53	1	1.53	2.96
x_3 linear	0.55	1	0.55	1.06
Quadratic	13.75	3	4.58	8.88 **
x_1 Quad.	5.16	1	5.16	10.01 **
x_2 Quad.	8.01	1	8.01	15.53 **
x_3 Quad.	0.56	1	0.56	1.09
Interaction	16.93	3	5.64	1.00
$x_1 * x_2$	16.40	1	16.40	31.79 **
$x_1 * x_3$	0.17	1	0.17	0.34
$x_2 * x_3$	0.04	1	0.04	0.08
Lack of fit	8.77	17	0.51	
Total	43.07	26		

* P = 0.05
** P = 0.01

Figure 33

Maximum likelihood ratios for various estimates of the power parameter α_1 for test series 3.

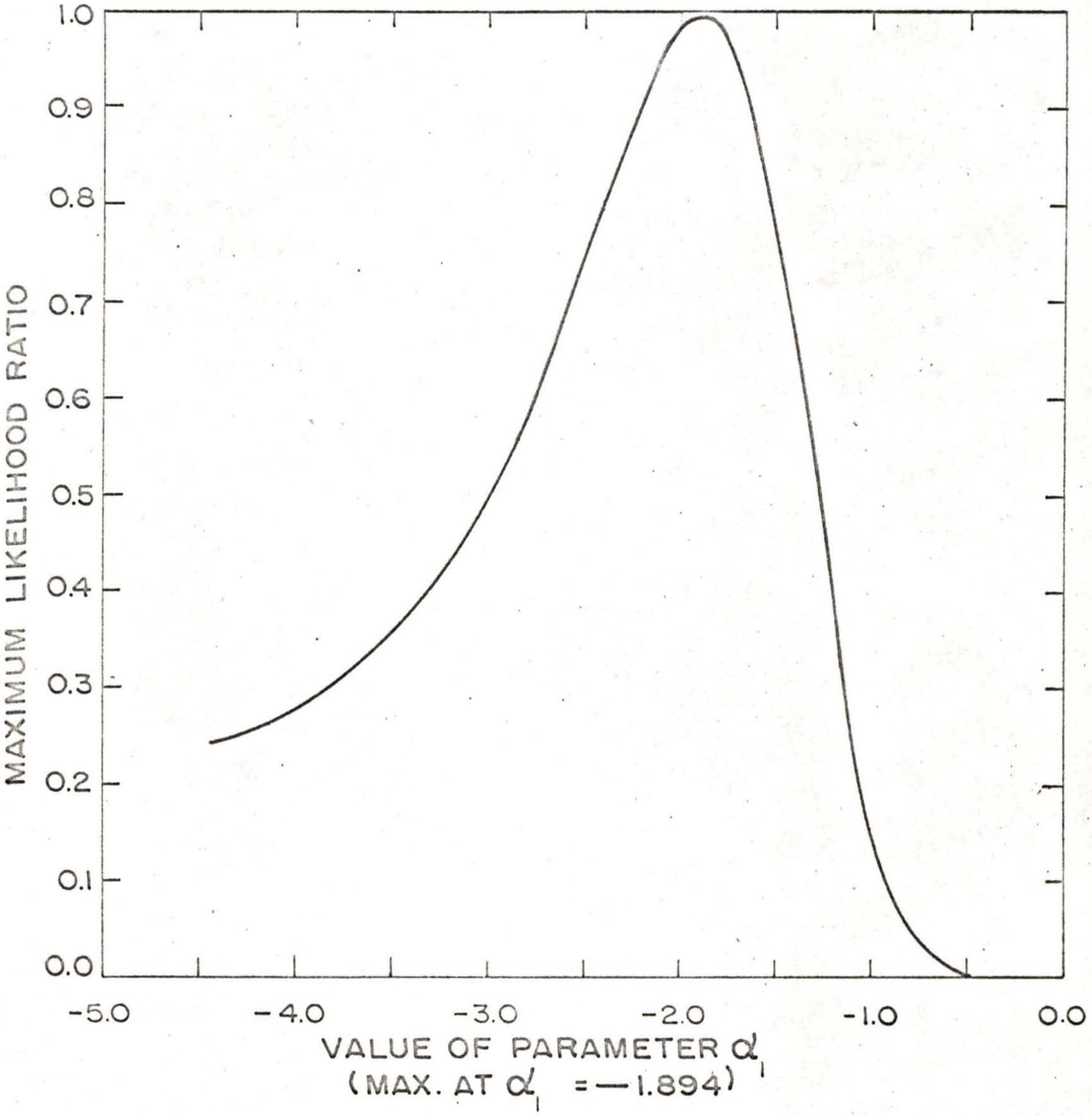
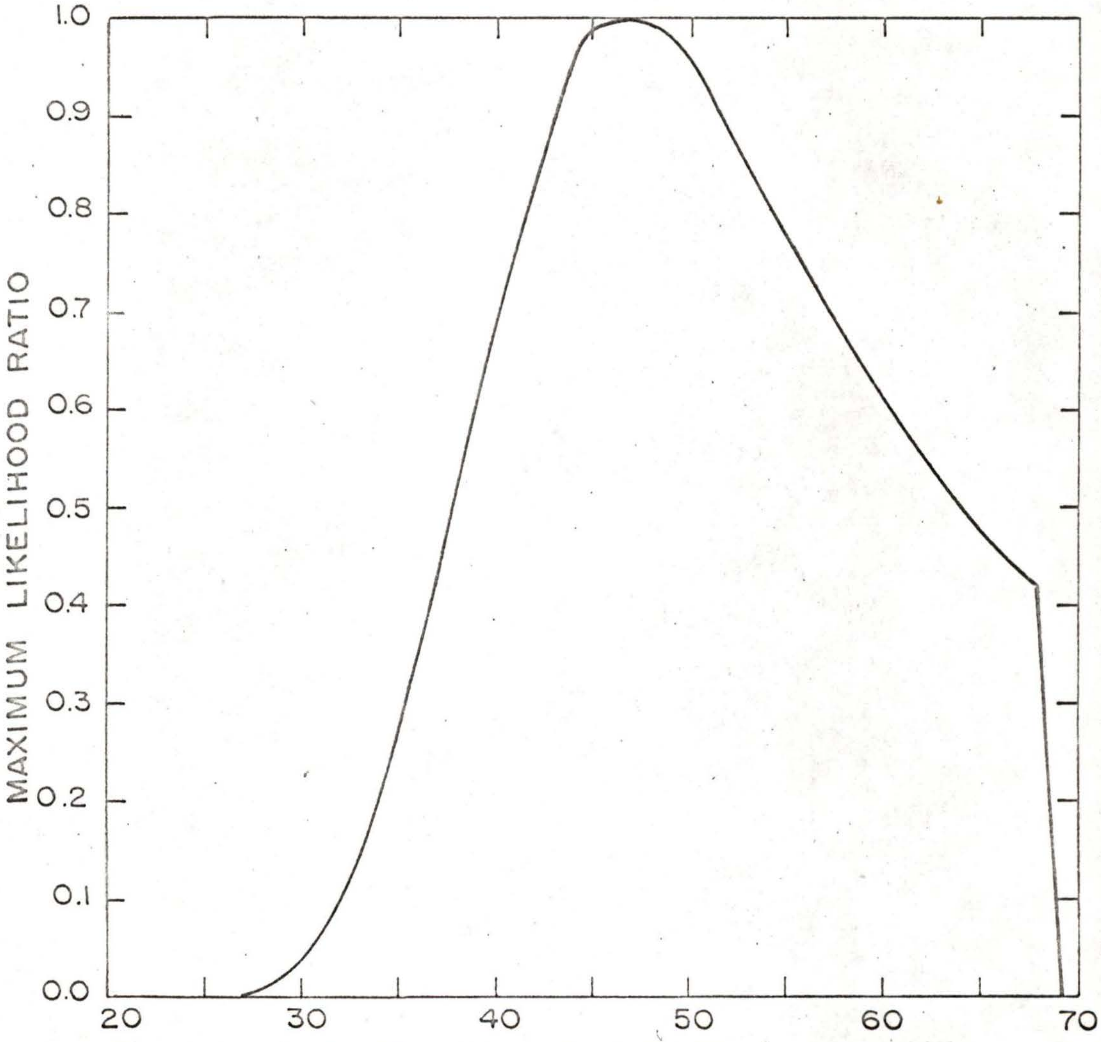

MAXIMUM LIKELIHOOD RATIO
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-5.0
-4.0
-3.0
-2.0
-1.0
0.0
VALUE OF PARAMETER α_1
(MAX. AT α_1 = —1.894)

Figure 34

Maximum likelihood ratios for various estimates of the power parameter α_2 for test series 3.



(MAX. AT α_2 = 4.690)

Figure 35

Maximum likelihood ratios for various estimates of the power parameter α_3 for test series 3.

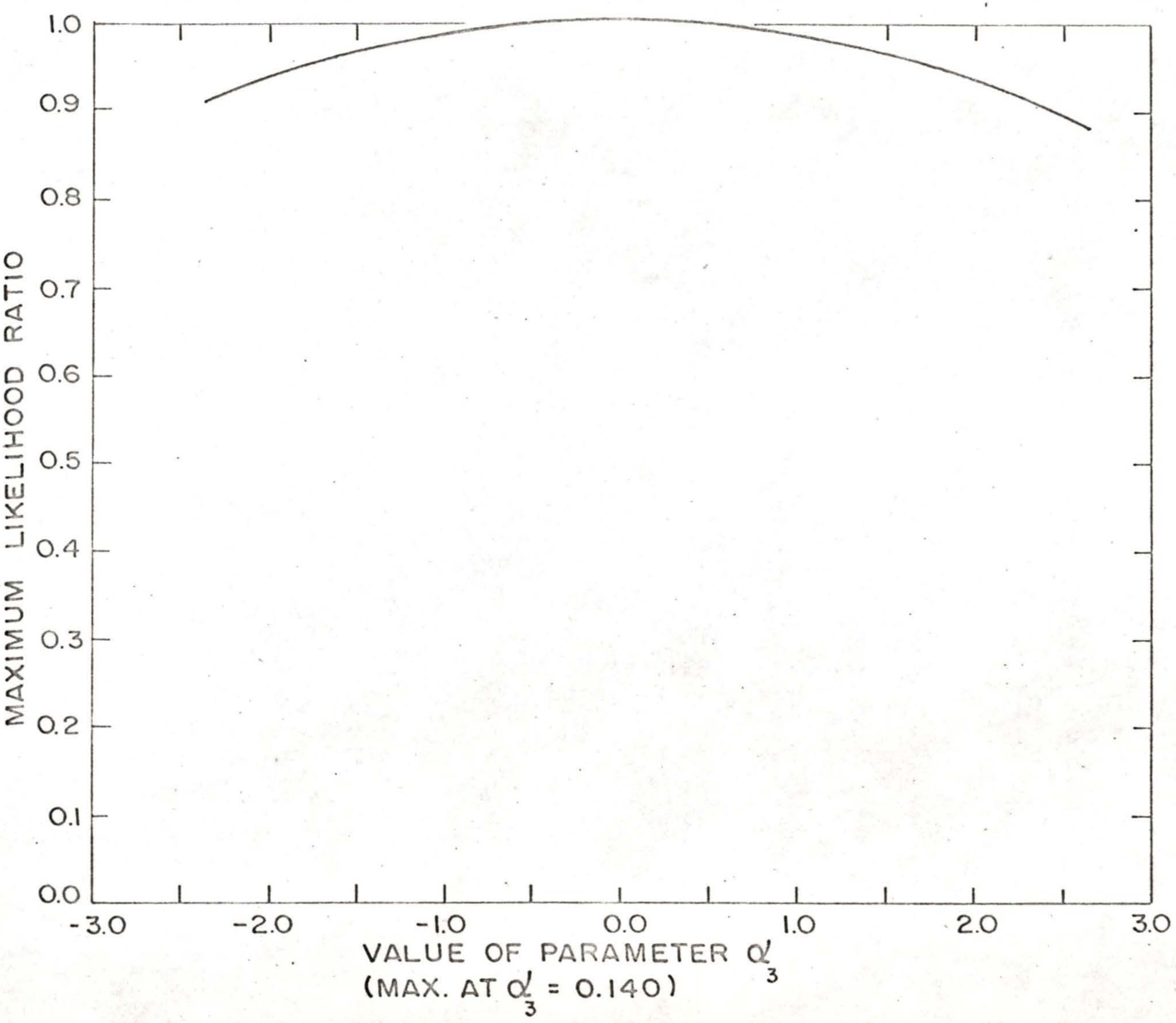

MAXIMUM LIKELIHOOD RATIO
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-3.0
-2.0
-1.0
0.0
1.0
2.0
3.0
VALUE OF PARAMETER α'_3
(MAX. AT α'_3 = 0.140)

Figure 36

Maximum likelihood ratios for various estimates of the power parameter γ for test series 3.

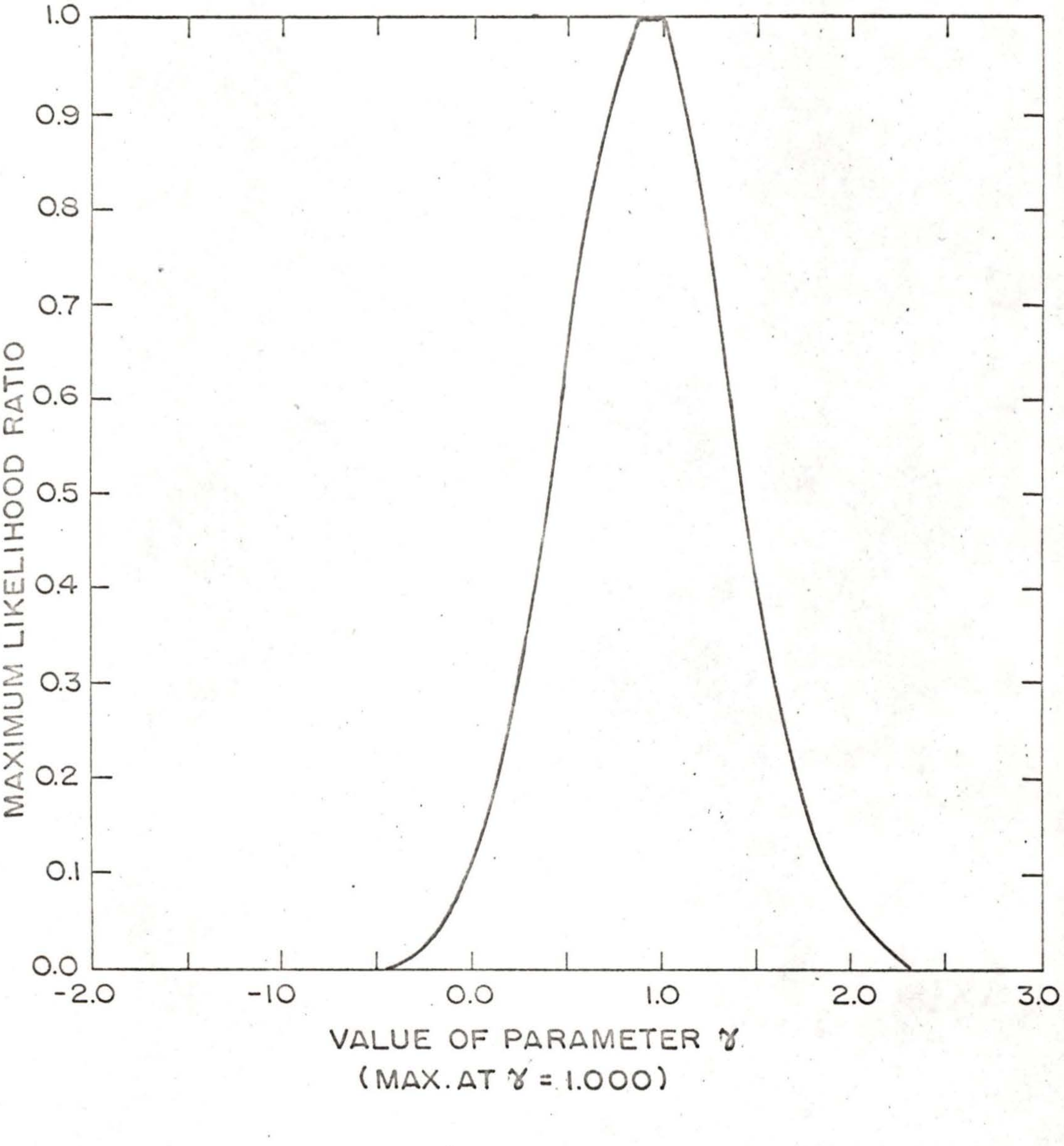

MAXIMUM LIKELIHOOD RATIO
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-2.0
-10
0.0
1.0
2.0
3.0
VALUE OF PARAMETER γ
(MAX. AT γ = 1.000)

Table XII. Analysis of variance of the transformed data from test series 3.

Source of Variation	SS	d.f.	MSS	Approx. F	MIR
Treatments	43.07	26	1.65	17.71	8.29×10^{-21}
Linear	5.83	3	1.94	20.81	4.89×10^{-11}
x_1 linear	5.63	1	5.63	60.24	7.30×10^{-11}
x_2 linear	0.00	1	0.00	0.04	0.96
x_3 linear	0.44	1	0.44	4.79	1.44×10^{-12}
Quadratic	11.79	3	3.93	42.05	1.26×10^{-13}
x_1 Quad.	1.89	1	1.89	20.23	3.14×10^{-6}
x_2 Quad.	9.49	1	9.49	101.54	1.75×10^{-13}
x_3 Quad.	0.39	1	0.39	4.26	2.17×10^{-2}
Interaction	24.47	3	8.15	1.00	1.30×10^{-18}
$x_1 * x_2$	23.76	1	23.76	254.19	1.88×10^{-18}
$x_1 * x_3$	0.07	1	0.07	0.83	0.43
$x_2 * x_3$	0.12	1	0.12	1.36	0.26
Transform	7.55	4	1.88	20.20	2.58×10^{-12}
Lack of fit	1.21	13	0.09		
Total	43.07	26			

could be removed without greatly affecting the adequacy of the model. The relative likelihood of the linear model providing an adequate fit to the data, as opposed to the non-linear model, was 2.58×10^{-12}. Hence, the non-linear model provided a more powerful test than the linear model, as a definite size effect could be discerned from the data. The canonical form of the polynomial was

$$Y - 9.393 = -162.756X_1^2 - 2.68 \times 10^{-12}X_2^2 - 3725.93X_3^2.$$

The centre coordinates of the non-linear model were estimated at:

acclimation temperature (x_1) = 7.70°C
test temperature (x_2) = 19.92°C
size (x_3) = 8.39 cm

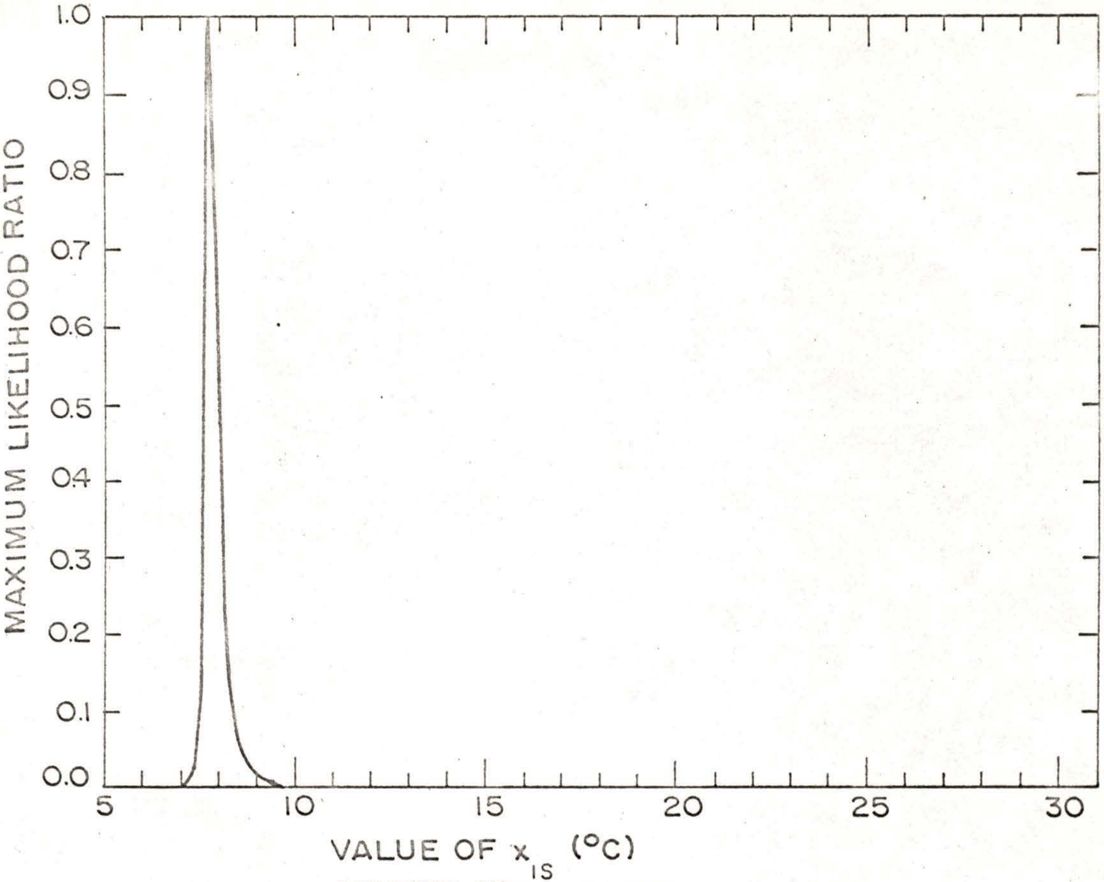
The swimming speed at the centre of the surface was calculated as 9.39 lengths/second. The x_1 and x_2 coordinates of the centre were very precisely estimated (Fig. 37) but the x_3 coordinate was poorly defined (Fig. 38).

The three factor non-linear response surface was illustrated by transects through the centre in the x_1, x_2, and x_3 planes. The swimming speed calculated at the centre of this surface appears somewhat unrealistic when compared with the observed data (Appendix III) and the more detailed surfaces developed for test series 1 and 2. Consequently, the maximum response isopleth plotted was 5.5 lengths/second. Comparison of the acclimation temperature-test temperature plot (Fig. 39) with the non-linear surfaces from series 1 and 2 suggests that the effects of these two factors have been poorly defined by the small series 3 design.

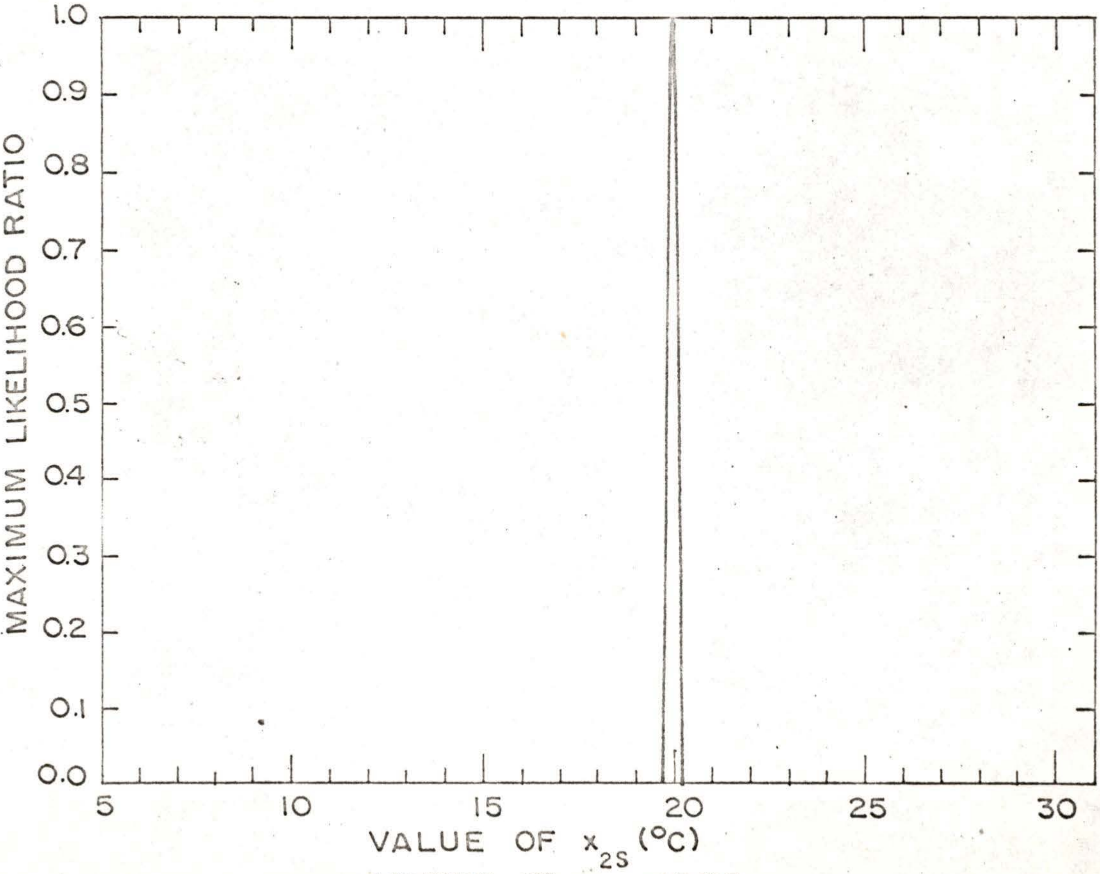
Within the size range investigated (approximately 7 cm. to 11 cm.) the non-linear plots indicate that the effect of size on performance was poorly defined (Figs. 40 and 41). The surface in

Figure 37

Test series 3; the non-linear model. Maximum likelihood ratios for various estimates of the centre coordinates. The acclimation temperature coordinate (x_{1s}) is shown in the upper panel, the test temperature coordinate (x_{2s}) in the lower.



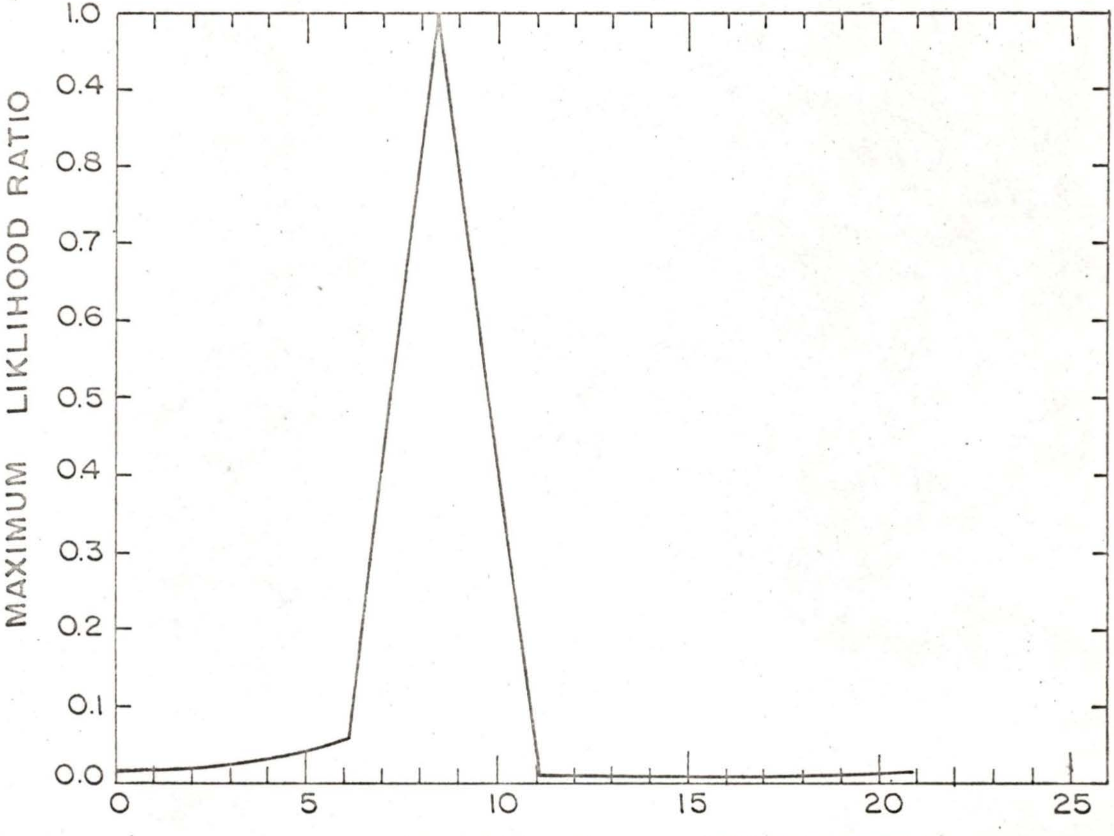
CENTRE AT $x_{1S} = 7.703$



CENTRE AT $x_{2S} = 19.92$

Figure 38

Test series 3; the non-linear model. Maximum likelihood ratios for various estimates of the centre coordinate x_{3s} (size).



CETRE AT $\hat{x}_{3S}$ =8.390

Figure 39

A transect through the non-linear model for test series 3, illustrating the effect of acclimation and test temperatures on swimming speeds for fish 8.39 cm. long. The isopleths indicate swimming speeds in lengths/second. The dotted lines indicate the area of the factor space encompassed by the experimental design.

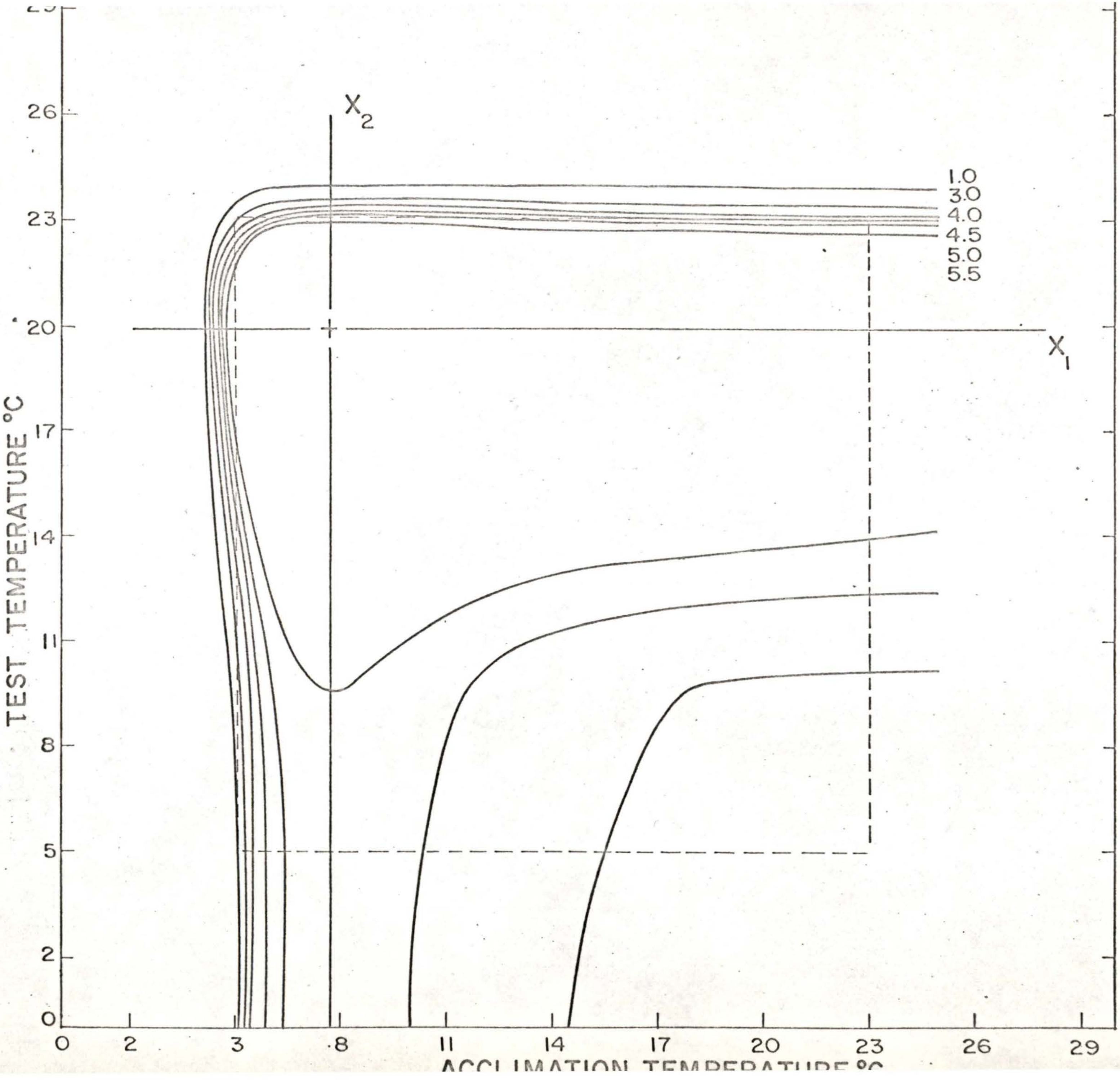

26
23
20
17
14
11
8
5
2
0
TEST TEMPERATURE °C
X$_2$
X$_1$
1.0
3.0
4.0
4.5
5.0
5.5
0
2
3
8
11
14
17
20
23
26
29
ACCLIMATION TEMPERATURE °C

Figure 40

A transect through the non-linear model for test series 3, illustrating the effect of acclimation temperature and size on swimming speeds for fish tested at 19.92° C. The isopleths are swimming speeds in lengths/second and the area of the experimental design is denoted by the dotted lines.

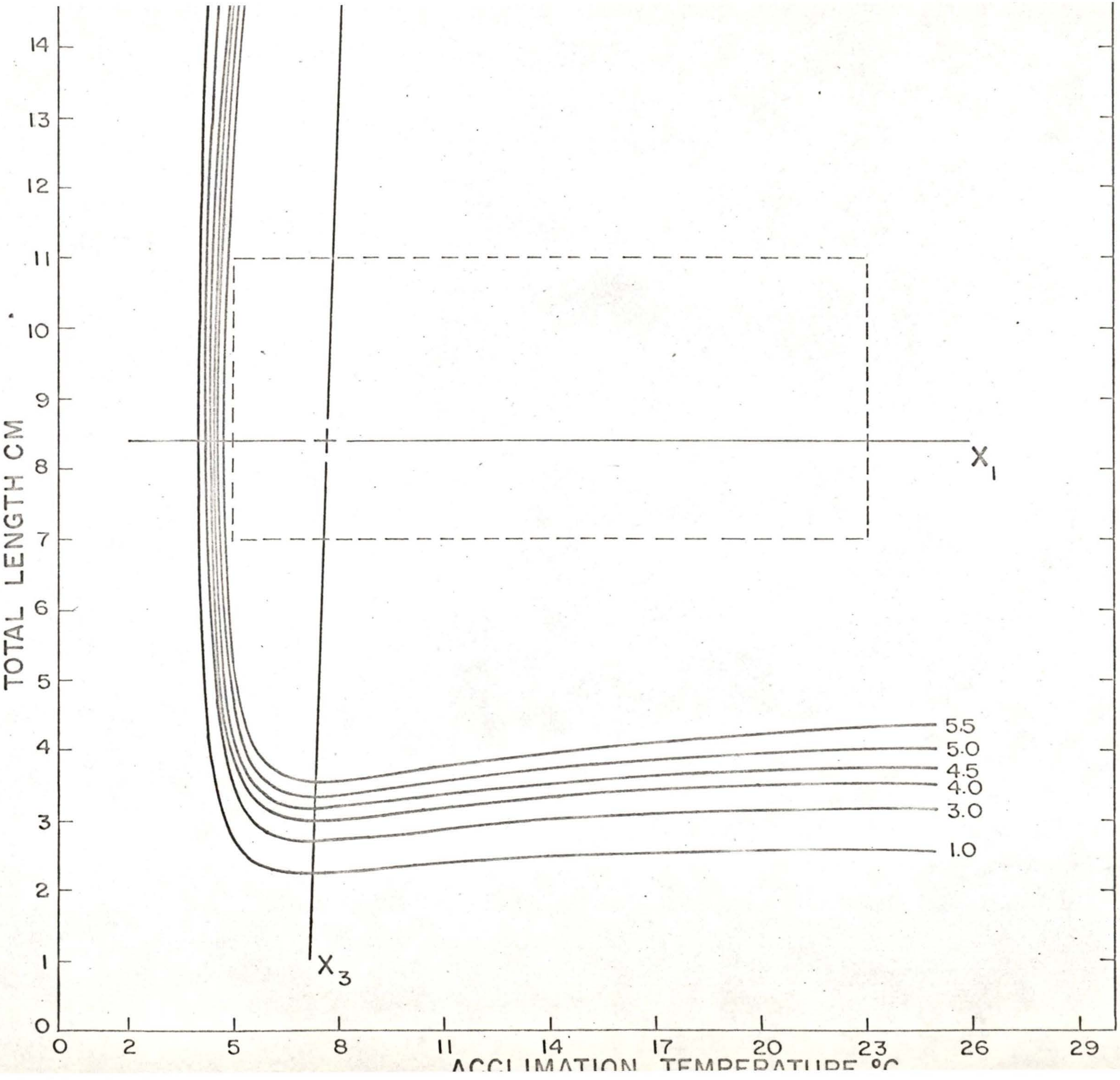

TOTAL LENGTH CM
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
0
2
5
8
11
14
17
20
23
26
29
ACCLIMATION TEMPERATURE °C
5.5
5.0
4.5
4.0
3.0
1.0
X_1
X_3

Figure 41

A transect through the non-linear model for series 3, illustrating the effect of test temperature and size on swimming speeds for fish acclimated to 7.70° C. The isopleths are swimming speeds in lengths/second and the area of the experimental design is denoted by the dotted lines.

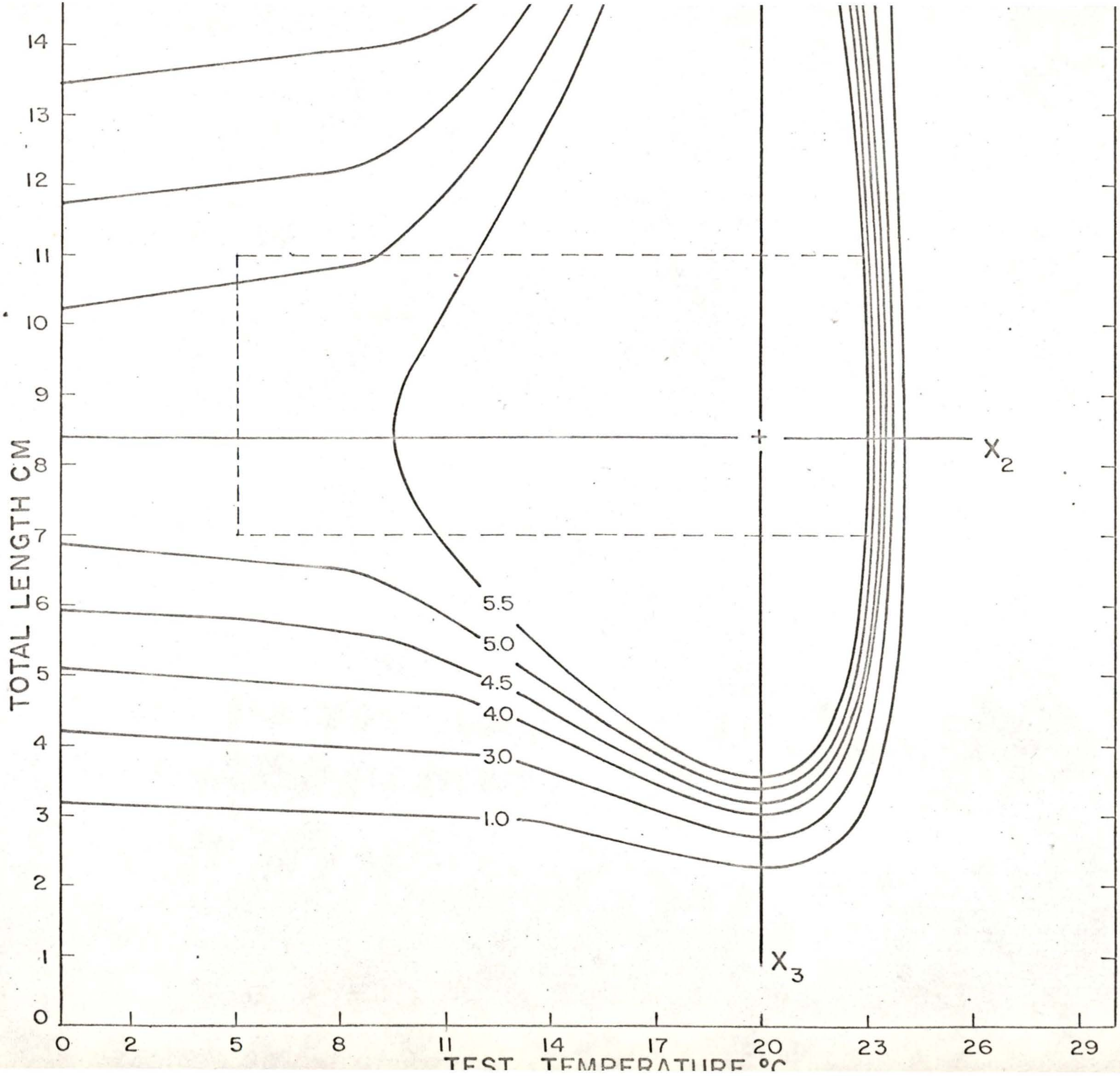

TOTAL LENGTH CM
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
0
2
5
8
11
14
17
20
23
26
29
TEST TEMPERATURE °C
5.5
5.0
4.5
4.0
3.0
1.0
X_2
X_3

Fig. 41 indicates that maximal performance occurred at a length of 8.4 cm. and that the effect of size was not constant at all test temperatures. However the response isopleths could not be accepted without reservation, as they appear to overestimate the swimming velocities actually observed in each of the three series.

Error Estimate

A t-test (Li, 1964) indicated that the results of day time and night time tests were not significantly different (Table XIII). The data from this series of repetitive tests was therefore combined to provide an estimate of experimental error. From the standard deviation of this test series, a variation of ± 7% could be expected for repeated tests at a given point. Assuming a constant variance throughout the factor space, this value is indicative of the error involved in the calculated response isopleths.

Post-Fatigue Mortality

Post-fatigue mortality occurred in 14 of the 170 swimming speed tests conducted in this study (Table XIV). The degree of mortality in these 14 tests averaged 25% and ranged from 10% (1 fish) to 100%. With the exception of three cases of single mortalities, post-fatigue mortality occurred only when test temperatures were above the upper temperature tolerance limits.

Table XIII. Comparison of day time and night time tests.

Swimming Speeds (lengths/second)

	Day time	Night time
	4.14	5.14
	5.06	4.62
	5.42	5.11
	5.07	5.24
Mean	4.92	5.03

<u>t</u> - <u>test</u>

t = -0.324 NS

(critical regions: t - 2.45; t 2.45)

Combined data: Mean (lengths/second) ± 1 standard deviation.

4.98 ± 0.36

Table XIV. Post-fatigue mortality

Acclimation temperature (° C)	Test temperature (°C)	Percentage mortality (10 fish/test)
23	27.5	100
20	26	10
20	26	20
20	5	10
17	26	30
17	26	30
11	14	10
8	23	10
5	23	10
5	23	20
5	23	20
5	23	30
5	23	40
5	5	10

DISCUSSION

Factors Affecting Swimming Performance

Experimental conditions.

On the basis of the error estimate, the median swimming speeds determined in this study appeared to be quite variable.

Genetic differences could have contributed to the variability observed, as the experimental fish were obtained from a wild population. Genetic variability might have been minimized by the use of offspring from a single female, but wild fish were used to obtain a wider representation of a natural population.

A further source of potential variability could arise from the handling of experimental fish during transfer from the acclimation tanks to the entry device. Fatigued sockeye require about 3 hours to recover sufficiently to perform at maximal levels. Following moderate levels of activity, sockeye recover from oxygen debt in about 1 hour (Brett, 1964). However, Black et al. (1962) demonstrated that normal blood and liver levels of pyruvate and lactate were not restored in rainbow trout until almost 12 hours after severe fatigue had occurred. Thus, while fish recover their swimming ability quite rapidly after fatigue, complete recovery requires considerable time. The fish in the present study were allowed one hour for recovery in the entry device prior to testing. Hence, recovery from the effects of handling could only be assumed complete at the time of entry into the test chamber.

The effect of group testing on the variability of the swimming speed response was not determined in this study. Brett (1965) reported that group testing of sockeye reduced metabolic rate variability through an averaging effect and a reduction in restless behavior and excitement. However, this may not have been the case with the coho, a more aggressive species. The level of aggressive behavior did not appear to be constant for all tests in the present study, and may have contributed to the variability between tests. Selection of fish according to size apparently reduced aggression, but this behavior appeared to be affected by other factors. For example, in test series 1, no aggressive acts were observed at test temperatures below 5° C. In test series 2 and 3, aggressive behavior was commonly observed at test temperatures as low as 2° C and may have caused some premature failures.

The dependence of swimming speeds on dissolved oxygen concentrations has been described by Davis et al. (1963). These authors demonstrated that the performance of underyearling coho is reduced at all oxygen levels below air saturation, but shows little or no improvement at levels above air saturation. The reduction in swimming speed is about 4% at oxygen levels as low as 80% saturation. The oxygen levels in the present study were generally maintained at air saturation ± 5% and only occasionally exceeded ± 10%. Therefore, it may be assumed that dissolved oxygen levels had little effect on the variability observed in this study. A more important effect of dissolved oxygen on performance could reside in the differential solubility of oxygen with respect to temperature. Thus, swimming ability at high temperatures will depend on the efficiency of oxygen extraction from an environment containing less dissolved oxygen (Brett, 1964) than is available at lower temperatures. However, this phenomenon would influence the level of performance with respect to temperature, rather than the variability associated with a given test.

Ancilliary variables.

In addition to the variations of experimental conditions, the effects of ancilliary variables on temperature-dependent swimming speeds should be considered.

The effect of size on swimming speeds of fish have been investigated by only a few authors (Table XV) but two basic patterns are apparent from the data. First, velocity may be directly proportional to size. Relative performance (lengths/second) is therefore independent of size. The dace and the roach are examples. Second, velocity may be dependent upon some fractional exponent of size. Relative performance thus decreases with increasing size. This relation is exemplified by the trout, goldfish, sockeye and sturgeon.

There appear to be several classes of physiological parameters influencing the relation between size and swimming performance. These are associated with a) the rate at which the fish produces energy, and b) the proportion of available energy that is required for swimming. The former is influenced by the amount of body musculature and the metabolic scope, the latter by those factors affecting hydrodynamic drag.

For the sockeye, both the percentage of body musculature and the metabolic scope increase with size (Brett, 1965). As the performance decreases, Brett concluded that the increased hydrodynamic drag accompanying larger size is only partially compensated for in

Table XV. The relation of size to swimming speed for various species of fish.

Species	Effect of size on swimming speeds Velocity proportional to:	Source
dace (*Leuciscus leuciscus*)	length 1.09	Bainbridge (1960)
trout (*Salmo irideus*)	length 0.58	Bainbridge (1960)
goldfish (*Carassius auratus*)	length 0.71	Bainbridge (1960)
sockeye (*Oncorhynchus nerka*)	length 0.49	Brett (1960)
Caspian roach (*Rutilus rutilus caspicus*)	length 1.0(approx.)	Pavlov et al.(1968)
Russian sturgeon (*Acipenser guldenstadtii*)	length < 1.0	Pavlov et al. (1968)

this species.

Bainbridge (1960) discussed several factors possibly affecting hydrodynamic drag. These included the roughness of the body surface, the fineness ratio (body form) and the Reynold's number (a length-velocity dependent frictional coefficient). While Bainbridge's data suggested that the Reynold's number may affect relative performance, his results were not conclusive.

The relationship between size and swimming performance developed by different authors may not be comparable, owing to differences in the methods and apparatus employed. The data of Pavlov et al. and Bainbridge (1960) were determined for burst speeds and were thus independent of metabolic scope (Brett, MS). As Brett's (1965) findings and those of the present study were determined for sustained speeds, comparison with the data of the former authors is difficult. Also, the factors affecting hydrodynamic drag may vary with the type of flow in the test apparatus. Hence, the results obtained from apparatus producing laminar flow (Bainbridge, 1960) may not be comparable with those obtained from apparatus producing turbulent flow (Brett, 1965; Pavlov et al., 1968; present study). More information, obtained under standardized conditions, is required before generalized conclusions may be drawn regarding the relationship of size to swimming performance.

The results of the present study did not clearly define the effect of size on the coho's performance at different test and acclimation temperatures. While a size effect is apparent from the non-linear model, quantification of this affect is difficult, as the model suggests levels of performance which appear unreal when compared with the observed data. This probably indicates that the size range employed in the present study (7 cm - 11 cm) was not great enough to detect real differences in temperature-dependent swimming speeds related to size. Further examination of this point would require a more extensive experimental design, replication of the design, or an expansion of the size range of test fish employed. The latter strategy would indicate, most economically, the presence or absence of a real difference. All three tactics would be required to adequately define the nature of the difference.

Seasonal changes in temperature-dependent responses have been demonstrated by a number of investigators. Comparison of temperature tolerance for winter and summer specimens of the red-bellied dace (Chrosomos eos) (Tyler, 1966) indicated a winter reduction of 2° C to 4° C in the upper tolerance boundary, depending upon the acclimation temperature. Hart (1952) demonstrated shifts in both upper and lower temperature tolerance levels for the yellow perch (Perca flavescens). The ultimate incipient upper lethal temperature (at the maximum possible acclimation temperature) was 3° C lower during the winter than during the summer. The lower lethal temperature at this acclimation temperature decreased by 5° C for winter specimens. Thus, it may be concluded that the dimensions of the tolerance domain are not fixed. A seasonal displacement, and possibly a seasonal change in the shape of the tolerance domain may occur.

Photoperiod appears to be a controlling factor in the seasonal change of temperature dependent responses. Hutchinson and Kosh (1965; quoted in Fry, 1967) indicated that a change in photoperiod from 8 to 16 hours produced a rise in the critical thermal maximum of the painted turtle (Chrysemys picta) equivalent to a 4° C increase in acclimation temperature. Goldfish exposed to a 16 hour photoperiod exhibited greater resistance to high temperatures than those exposed to an 8 hour photoperiod (Hoar and Robertson, 1959). The difference was greatest during the spring and fall. Goldfish exposed to the 8 hour day-length were more cold-resistant than the 16 hour fish from October to December, but the nature and magnitude of this response varied at other periods of the year. The authors suggest that these seasonal resistance changes would have survival value during the spring and fall periods of rapid temperature change.

Seasonal changes in metabolic rate have also been observed. When compared at equal temperatures, the standard metabolism of Fundulus parvipinnis rose during the winter and decreased during the summer (Wells, 1935). For a given temperature, the routine metabolism of the pinfish (Lagodon rhomboides) is higher in winter than in the summer (Wohlschlag et al., 1968). However, Ekberg (1958) found that gill tissue respiration of goldfish was higher in summer than in winter, when compared at equal temperatures. No photoperiod effect was apparent for gill tissue of the crucian carp (Carassius carassius), but the whole fish had a higher metabolic rate at 20° C when photoperiod was increased from 7 hours to 17 hours (Roberts, 1960). Investigation of the seasonal rates of standard metabolism for the brook trout (Salvelinus fontinalis) and the brown trout (Salmo trutta) (Beamish, 1964) indicated that the seasonal rise in metabolism coincided with the reproductive periods of these species. Thus, seasonal changes in metabolic rate may be only indirectly related to seasonal temperature changes.

Preferred temperatures in fish also show seasonal variation. A sudden increase in the thermal preferendum of the brook trout was observed in late winter (Sullivan and Fisher, 1953). Mantleman (1958) described a decrease in the preferred temperature of the rainbow trout (Salmo irideus) during the fall.

It has been suggested by Fry (1964, 1967) and Brett (1965, MS) that the thermal preferendum appears to indicate the optimum temperature for activity in those species for which activity and the temperature preferendum have been measured in relation to acclimation temperature. Thus, seasonal changes in temperature preferenda may be indicative of seasonal changes in temperature-dependent swimming speeds.

As the fish in the present study were exposed to natural variations in photoperiod, some evidence of seasonal changes in swimming speed may be obtained from examination of the response surfaces. The dynamic properties of biological response surfaces with respect to season are clearly shown by Alderdice (1963a, MS). Response surfaces relating survival times of juvenile coho salmon exposed to 3 mg./l sodium pentachlorophenate at different levels of temperature and salinity showed seasonal changes in the temperature-salinity interaction (rotation of the surfaces), changes in the position of the centre point (translation of the surfaces with respect to both temperature and salinity) and changes in the absolute survival time (capacity changes at the centre of the surfaces). With respect to temperature, the optimal temperature for survival was 4.2° C during August/September (fry stage), 2.7° C during April/May (smolt stage) and 4.9° during July/September of the second summer (post-smolt stage).

The seasonal changes observed by Alderdice (1963a) and the results of the present study may have been influenced by several seasonally-related factors, including a) adaptations to seasonal temperature changes, and b) physiological and morphological changes in the developmental stages of the coho, in preparation for migration to a marine environment. With this limitation in mind, the non-linear response surfaces for the present study (test series 1, September/January and test series 2, January/April) may be compared for evidence of seasonal changes in swimming speed. Comparison of performance near the temperature tolerance boundaries indicates (Figs. 18 and 27) that fish in test series 2, when acclimated to temperatures from 5° C to 17° C, were better able to perform (than those in test series 1) at temperatures near or above the upper temperature tolerance boundary. The performance of the former group at temperatures near or below the low temperature tolerance boundary (as low as 2° C) was reduced from that of the test series 1 fish. These changes would appear to be beneficial to organisms subject to the rising habitat temperatures normally encountered at the time of the series 2 experiments.

The comparison further suggests that a translation of the response surface centre to slightly lower coordinates of acclimation the test temperature has occurred in test series 2. Thus, fish acclimated to temperatures of 20° C. or below in test series 2 may have been better able to swim than those in test series 1. However, the maximum likelihood plots indicate that the centre coordinates were not defined precisely enough to determine whether the observed translation of the centre was real.

The ridge of maximal performance in relation to acclimation temperature (Figs. 20 and 28) also suggests seasonal differences between the test series. While the position of the ridge is almost identical in both series, the height of the ridge is greater in series 2, when considered over the acclimation temperature range of 5° C to 17° C. In relation to test temperature, the ridge is also broader in series 2 for the 2° C to 17° C acclimation temperature range. These differences may be interpreted as a greater ability of the series 2 fish to swim at moderately warm temperatures. Such a change during periods of rising temperatures would appear to have survival value.

In summary, some of the differences in the non-linear response surfaces fitted to test series 1 and 2 might be attributed to seasonal changes in temperature dependent swimming speeds. The differences may be described as an inner rotation or change in the shape of the response surface, appearing to involve fish acclimated from 5° C to 17° C. The data suggest an increased ability of the series 2 fish to perform at temperatures near or above (for the test period) the upper tolerance boundary, combined with an increased ability to perform at moderately warm temperatures within the tolerance zone. This facilitation of performance at warmer temperatures is apparently accompanied by a decrease in performance at temperatures near or below (for the test period) the low temperature tolerance boundary.

However, as the error estimate indicates that the response isopleths may be subject to an error of about 7 percent, the small seasonal effects suggested by the data have not been precisely defined.

There are a number of reasons why seasonal differences discussed were not clearly defined. The magnitude of seasonal changes in temperature dependent responses may vary with both the response and species in question. Fry (1967) stresses the fact that differences in swimming speeds are relatively small, compared with other temperature-dependent responses such as metabolic rate. Also, the difference in size of test fish employed in series 1 and 2 may partially have masked seasonal variations. However, the time periods required for the completion of each test series, and the lack of a distinct time period between these series were probably the most important factors preventing a clear definition of seasonal changes in swimming performance.

A refined definition of seasonal changes would require a comprehensive investigation involving several considerations. A detailed study of the shape of the temperature-swimming speed surface (as determined in the present study) would first be required. The relation of size to swimming speed must also be clearly defined, in order to remove the effects of this variable from seasonal data. A reduced experimental design, capable of being completed in less than a month might then be employed a number of times throughout the year to determine seasonal changes in swimming speed. The size of this design is critical. For example, in test series 3, nine combinations of acclimation and test temperatures were employed. The non-linear surface fitted to the series 3 data indicates that a more extensive design is required to adequately describe THE whole response domain of *O. kisutch*. A design of 25 to 30 points may be required to adequately define the temperature performance domain of this species. Nevertheless, restricted regions of the domain, such as the ridge of maximal performance or the areas near the tolerance boundaries may be investigated with smaller designs.

Temperature

The non-linear response surfaces fitted to test series 1 and 2 of the present study (Figs. 18 and 27) clearly demonstrate that swimming speeds of juvenile coho are affected by both acclimation and test temperatures. Acclimation modifies the response to environmental (test) temperature in such a way that the coho is able to maintain a greater constancy of swimming speed at all temperatures than would be expected if acclimation were not present. Thus, the coho is able to maintain a moderate level of performance over most of its tolerance domain.

The most obvious features of the coho's temperature-swimming speed response surface are a) the temperature optimum, which at 20° C is surprisingly close to the upper temperature tolerance boundary, and b) the presence of a rising ridge leading to this optimum. Interaction of test and acclimation temperatures is such that the temperature producing optimal performance occurs at about 16.5° C for 2° C acclimated fish, and rises until acclimation and test temperatures coincide at about 20° C. The shape of this ridge indicates that the interaction of test and acclimation temperatures is not constant. If it were constant, the ridge would be symmetrical. However, curvature of the axis of this ridge (test series 2) and displacement of the response isopleths toward lower test temperatures indicate that non-linear interactions of acclimation and test temperatures occur.

Detailed response surfaces relating acclimation and test temperatures to performance are not available for other species. However, some of the data in the literature may be interpreted in terms of response surfaces.

The data of Benthe (1954; quoted in Precht, 1958) suggest that the effect of acclimation and test temperatures on the excitability of the foot of Limnaea stagnalis may be described by a ridge system. The maximum observed response occurred at about 17° C for 12° C acclimated specimens. As the acclimation temperature increased to 21° C, the temperature producing maximum response rose to 24° C, but the magnitude of the maximum was smaller than that observed for 12° C acclimated specimens. As only 3 transects of this surface are available, a detailed description is not possible.

The heat resistance of stomach juice proteolytic activity from Helix pomatea (Mews, 1957; quoted in Precht, 1958) is modified by acclimation temperature. Although the data are limited they suggest the presence of a complex rising ridge system which may contain two maxima at higher acclimation temperatures.

As these examples refer to responses of limited systems within organisms, they may not be indicative of the integrated response of the whole organism.

Response surfaces have been fitted by eye to two sets of data relating acclimation and test temperatures to performance (Alderdice, MS). The surface fitted to the data of McLeese and Wilder (1958) indicates that the walking rate of the lobster (Homarus americanus) is modified by both acclimation and test temperatures. The contours of this surface clearly indicate that the interaction of test and acclimation temperatures is not constant. A rising ridge is apparent in this surface. The maximum walking rate of lobsters acclimated to low temperatures occurs at temperatures higher than those of acclimation when walking rate is measured acutely. Thus, maximum walking rates occur when the lobster acclimated to 2° C is exposed to a temperature of 6° C. As acclimation temperature is increased, the temperature at which maximum performance occurs approaches the level of the acclimation temperature. Finally, at temperatures above 20° C, the lobster performs maximally at its acclimation temperature. Furthermore, there are two distinct regions of optimum performance on this response surface. The first occurs at an acclimation temperature of about 15° C and a test temperature of about 17° C. The second occurs at acclimation and test temperatures of about 25° C, quite near the maximum upper lethal temperature (32° C).

The second response surface, fitted by Alderdice (MS) to the data of Fry and Hart (1948b) illustrates the known dependence of cruising speed for the goldfish (Carassius auratus) upon both acclimation and test temperatures. This surface also contains a rising ridge. Maximum performance of 5° C acclimated fish occurs at about 17° C and the axis of the ridge rises gradually with increasing acclimation temperatures. At an acclimation temperature of 20° C, the test temperature producing maximal performance is slightly higher than 20° C. At this point, the axis turns and parallels the equal acclimation-test temperature diagonal. The nature of this ridge clearly indicates that the interaction of test temperature and acclimation temperature is non-linear. The surface also indicates that two swimming speed optima may occur for the goldfish. The first occurs at an acclimation temperature of about 25° C and test temperature of about 27° C. The second occurs at an acclimation temperature of about 35° C and a test temperature of about 37° C. Again, this second centre is close to the maximum upper lethal temperature.

Data of Ferguson, (quoted in Fry, 1964) for the yellow perch (Perca flavescens) suggests that the response surface for that species contains a rising ridge. The axis of the ridge (maximum performance) occurs at about 18° C for perch acclimated to 9.3° C and rises to about 26° C for 20° C acclimated specimens. The axis then rises sharply to 30° C for 25° C acclimated fish, suggesting a non-linear interaction of test and acclimation temperatures.

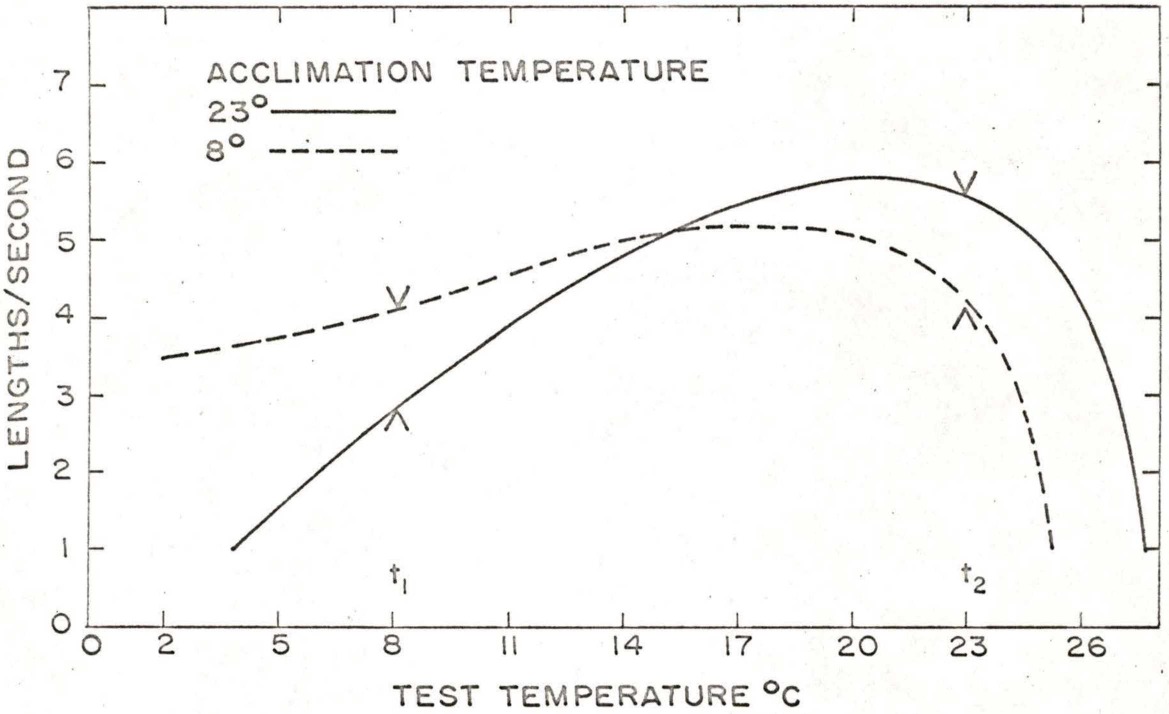
The available data suggest that ridge systems may be common in acclimation-test temperature response surfaces. Acclimation temperature-test temperature interactions may frequently be non-linear. In some cases, surfaces may contain more than one response centre. However, detailed response surfaces for a number of species will be required before a detailed description may be made of the manner in which these two variables affect performance.

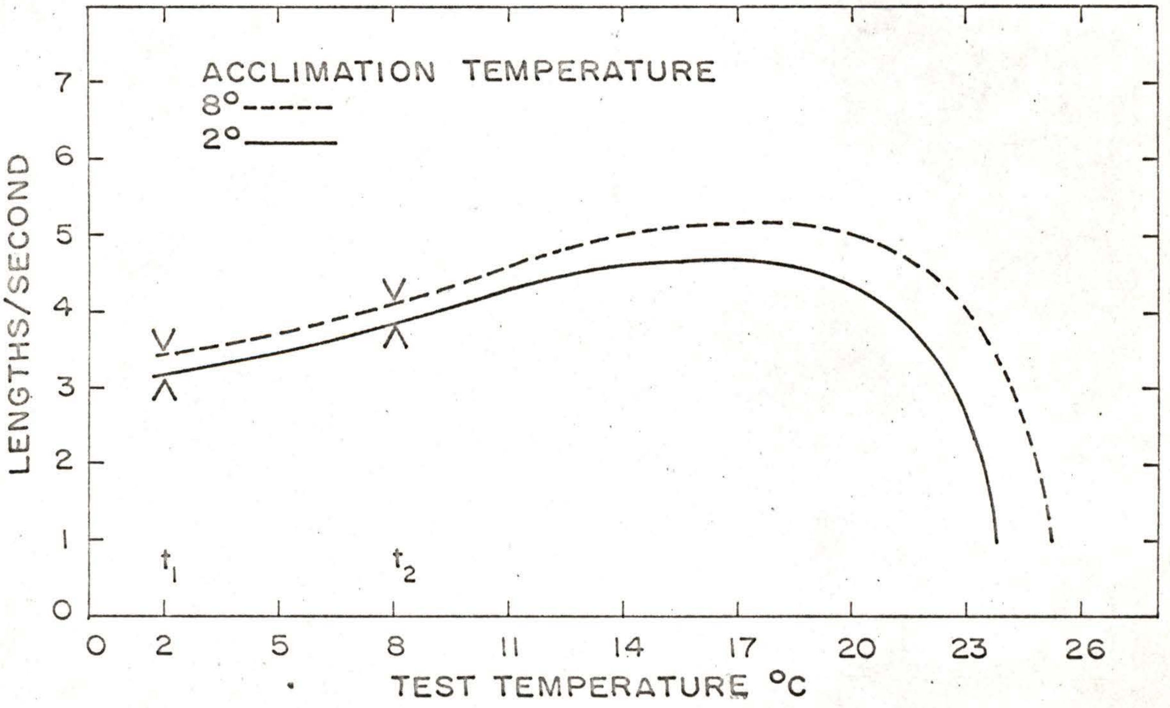
It is interesting to evaluate the coho response surface in terms of temperature adaptation types as described by Precht (1958). Precht distinguishes a number of types according to the change in response (eg. oxygen consumption) which occurs when an organism is taken from a temperature to which it is acclimated (t_1) and put at another (higher or lower) temperature (t_2). After acclimation has occurred at the new level, the response may diminish, increase, or remain at the level reached immediately following the initial change to the new temperature. Precht distinguishes between these patterns of adjustment and assigns them characteristic names.

For the coho in this study, transects were taken through the non-linear surface calculated from the test series 1 data (Fig. 42). The upper panel of this figure compares transects taken through the

Figure 42

Transects through the non-linear response surface fitted to data from test series 1. See text for further explanation.


ACCLIMATION TEMPERATURE
23°
8°
LENGTHS/SECOND
0
1
2
3
4
5
6
7
TEST TEMPERATURE °C
0
2
5
8
11
14
17
20
23
26
t1
t2


ACCLIMATION TEMPERATURE
8°
2°
LENGTHS/SECOND
0
1
2
3
4
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6
7
TEST TEMPERATURE °C
0
2
5
8
11
14
17
20
23
26
t1
t2

response surface at acclimation temperatures of 8° C and 23° C. The transects indicate that if the coho is acclimated to 8° C (t_1), its swimming speed will remain nearly constant after transfer to 23° C (t_2). After the fish becomes acclimated to the new temperature its swimming speed will rise to a rate above the 8° C acclimated rate. This acclimation pattern differs from all of Precht's adaptation types, although his type 5 (inverse compensation) is somewhat similar. However, if the coho is first acclimated to 23° C (t_2), the swimming speed will at first drop after transfer to 8° C (t_1) and then rise to an intermediate level after acclimation to the new temperature is complete (partial compensation, Precht's type 3).

Examination of the lower panel of Fig. 42 indicates that coho acclimated to 2° C show a rise in performance after transfer to 8° C and the swimming performance further increases as they become acclimated to the new temperature (Precht's type 5). Furthermore, those fish acclimated to 8° C exhibit a drop in swimming speed after transfer to 2° C and performance continues to drop as acclimation proceeds (Precht's type 5).

In the terms outlined by Prosser (1958), the upper panel of Fig. 42 is indicative of a clockwise rotation of the swimming speed curves. The lower panel, however, suggests a translation of the swimming speed curves to the right, but without rotation.

This example clearly indicates the need for development of detailed response surfaces to fully appreciate the action of acclimation and acute temperature experience on temperature-dependent responses. Precht's adaptation types and Prosser's acclimation patterns consider only pairs of transects across a response surface. However, adaptation types or acclimation patterns are seen to be dependent upon both the nature of the response surface in question and the particular temperature levels selected by the investigator.

The occurrence of two activity maxima in the response surfaces constructed for the lobster and the goldfish (Alderdice, MS) presents an intriguing problem. It is suggested by Alderdice that the maxima occurring at lower temperatures may reflect physiologically optimal temperatures for these species, provided that other objective measures of functional capacity coincide with these maxima. The upper maxima appear to provide the animals with a high capacity to move at near-lethal temperatures, presumably increasing their changes of encountering lower, more favourable temperatures. Fisher and Sullivan (1958) observed a bimodal temperature response in the locomotion of the speckled trout (_Salvelinus fontinalis_). Removal of part of the cerebellum resulted in a disappearance of the lower maximum, but not the higher maximum. This suggests that the lower maximum may be a response of the integrated organism, while the higher maximum may be associated with the general irritability of nervous tissue.

Sufficient data are not yet available to determine whether double maxima are common in temperature-activity relations. The swimming speeds of _O. kisutch_ determined in the present study showed no evidence of two maxima. However, it is noted that the lower response maxima observed for the speckled trout, the lobster and the goldfish all occurred near the centres of their respective tolerance domains. As the single maximum of the coho occurred near the upper limits of its tolerance domain, the presence of a second, slightly higher maximum (if one existed) would be difficult to detect.

Multiple Responses and Ecological Considerations

Final temperature preferenda (selected temperature = acclimation temperature) appear to be correlated with various activity optima for a number of species. The final preferendum (25° C) for the guppy (Lebistes reticulatus) coincides with the temperature producing maximal resistance to high lethal temperatures, as well as the growth rate optimum. The maximum response of Atlantic salmon (Salmo salar) to an electrical stimulus occurs in the region of the preferred temperature (Fisher and Elson, 1950; quoted from Brett 1956). The suggestion that preferred temperatures may indicate conditions favourable to activity has been further developed by consideration of the goldfish cruising speed surface (Alderdice, MS). The position of a ridge of preferred temperatures at acclimation temperatures below the final preferendum suggests that the rising ridge of performance in this surface may be correlated with preferred temperatures. Comparison of the preferred temperatures of the yellow perch with the position of its performance ridge (Ferguson; quoted from Fry, 1964) suggests that for the yellow perch, these two responses may also coincide.

On the basis of these data, it would be reasonable to expect the temperature preference of the coho to coincide with the axis defining temperatures producing maximal performance for each acclimation temperature, that is, the major ridge of the coho response surface. However, only one point on the coho's preferred temperature curve has been defined (Brett, 1952). This single point indicated that the preferred temperature of 10° C acclimated fish was only slightly above the acclimation temperature. If optimal activity and preference actually are related for this species, a preferred temperature near 18° C would be expected at this acclimation temperature. A more detailed description of the preferred temperatures of O. kisutch in relation to acclimation is required before further conclusions can be drawn.

Fry (1964, 1967) indicated that at a given test temperature, those fish acclimated to that temperature show the best possible performance. This appears to be a reasonable statement when the data examined (Carassius auratus, Perca flavescens, Salmo salar and Notropis cornutus) are viewed as transects of a temperature surface (Fry, 1964, 1967: his Figs. 4 and 8 respectively). Interpretation of these surface transects is rather difficult as the response to a given test temperature may be very similar, yet not identical, for a number of acclimation temperatures. Interpretation is enhanced when these data are plotted as response surfaces. For example, the response surface plotted by eye for the goldfish data (Alderdice, MS) suggests that conditions producing the ultimate maximum cruising speed may not be those of equal acclimation and test temperature. The plotted surface suggests that the ultimate maximum cruising speed appears to be restricted to an area slightly above the temperature diagonal. Calculation of a non-linear response surface for the goldfish data (Lindsey et al., MS) further suggests that the "eyed" response surface may be correct, as the calculated centre and near-maximum swimming speeds are displaced above the temperature diagonal. Nevertheless, maximum likelihood plots of plausible alternative temperature loci indicate that the centre has not been estimated precisely enough to define a real difference.

The response surfaces in the present study also suggest that the acclimation temperature producing maximal response for a given test temperature may be other than the test temperature. This is most noticeable at very low test temperatures (2° C). Fish acclimated to temperatures from 6° C to 8° C appear better able to perform at the former temperature than 2° C acclimated fish. The size of the error estimate in the present study indicates that this difference may be real.

A possible explanation of this phenomenon is suggested from field observations. During the winter, temperatures in coastal streams are often below 2° C. Coho in these streams appear to overwinter by burrowing into the bottom debris, remaining there in a semi-dormant state (Wickett, pers. comm.). A low metabolic rate would be advantageous during this period, as coho in their natural environment are not actively swimming during periods of extreme cold. Thus, the drop in performance at all temperatures observed for 2° C acclimated fish may have been due to a decrease in metabolic rate associated with the normal overwintering process. This suggests a fundamental change in the nature of the acclimation process. The non-linear response surfaces indicate that over the range of 23° C to 8° C for test series 1 and 23° C to 6° C for test series 2, acclimation provides the coho with maximum or relatively high performance capability. Thus this poikilotherm is "relatively" independent of temperature in this range with respect to its level of performance, and approaches a state which might be called pseudohomeothermy. On the other hand, when the coho is acclimated to temperatures below 6° C to 8° C, its performance at all test temperatures is decreased. The possible significance of this 6° C to 8° C range of temperatures is again suggested from field observations. Seaward migration of coho smolts in the spring usually begins when temperatures rise above about 6° C (Wickett, pers. comm.), and emergence from the bottom debris may occur slightly below this temperature.

Interpretation of the acclimation surface as suggested above remains somewhat speculative. Nevertheless, the concepts outlined correspond with field observations. Detailed investigation of the metabolism and performance of overwintering coho might determine whether the apparent change in the acclimation process at low temperatures is related to the overwintering behavior.

Alderdice (MS) has suggested that a number of important physiological responses to a variable or group of variables may define physiological optima for a species. For example, the final preferendum and the ultimate maximum cruising speed of the goldfish coincide at a test temperature of 28 to 29° C when acclimated to 25° C (Fry, 1947; Fry and Hart, 1948b). Furthermore, maximum metabolic scope (Fry and Hart, 1948a), as measured on the temperature diagonal (maximum 26° C to 28° C) lies very close to the maximum for cruising speed and final preferendum. Thus, temperatures from 25 to 29° C might be considered a physiological optimum for _Carassius auratus_ with respect to preference, swimming performance and metabolic scope.

The data available for the sockeye (O. nerka) may also be considered. A complete acclimation temperature-test temperature response surface for swimming speed is not available. However, experimental points have been determined along the acclimation temperature-test temperature diagonal (Brett, 1964) and on an acutely determined transect for an acclimation temperature of 15° C (Brett, 1967). These points indicate that maximum swimming speed occurs on the presumed surface at about 15° C. Metabolic scope of the sockeye (Brett, 1964) is maximal at 15° C. When the fish were provided with excess rations, maximal growth of this species also occurred at 15° C (Brett et al., 1969). The data of Brett (1952) suggest that the final preferendum of O. nerka is slightly below this temperature. Thus, in terms of swimming capacity, metabolic scope, growth on excess rations and temperature preference, 15° C may be a physiologically optimal temperature for the sockeye. On the other hand, maximum net food conversion efficiency for this species occurs at approximately 8 to 10° C, and is still quite high at temperatures as low as 5° C (Brett et al., 1969). Maximum growth on reduced rations also occurs at successively lower temperatures (Brett et al., 1969).

Comparison of Brett's data with field observations indicates that the sockeye fully exploits this temperature-dependent physiological potential. Young sockeye feed at the surface of Babine Lake, B.C. at dusk, in water temperatures near 15° C, and retreat to deep water, some 10 degrees colder, during the day (Narver, 1967). Thus, capacity for activity of juvenile sockeye is greatest while they are feeding in the surface waters. Digestion occurs in colder water, where reduced metabolic requirements allow more efficient utilization of food.

The present study has indicated that maximum performance of the coho occurs at a relatively warm temperature (20° C). Performance of this species at temperatures near the upper tolerance boundary remains high. Considerable ability to perform at temperatures as much as a degree above the upper tolerance boundary may be maintained for 8 to 10 hour periods of exposure. These attributes, combined with the ability to modify performance through acclimation, suggest that the coho is well-equipped to occupy warm habitats. The lower performance optimum of the sockeye (15° C) and the sockeye's presumed greater ability to perform at low temperatures appear to be major differences between the two species regarding temperature-dependent swimming capacity. Also, post-fatigue mortalities of coho in this study were generally limited to temperatures above the upper tolerance boundary. Post-fatigue mortalities of sockeye were commonly observed by Brett (1964; his Fig. 19) at temperatures slightly below the upper tolerance boundary of this species. Thus, exposure to near-lethal high temperatures may be less harmful to the coho than the sockeye.

Certain tentative assumptions might now be advanced on the basis of the knowledge gained on the performance of coho in this study, and by comparison with the data discussed regarding temperature-dependent responses in the sockeye and the goldfish. Maximum metabolic scope and growth maxima on excess diets for coho might be expected to coincide with the performance maximum at 20° C. It is further suggested that preferred temperatures of coho may coincide with the ridge defining maximum performance for each acclimation temperature. However, with the exception of swimming speed, the effects of temperature on these other responses for coho have yet to be more fully defined. Thus, a better understanding of the ecological implications of the effects of temperature on _O. kisutch_ appears to await a fuller development of knowledge on temperature-dependent responses, as well as a better understanding of the interrelations which may exist between these responses.

SUMMARY

1. The effects of acclimation and acute temperature experience on the sustained swimming performance of juvenile coho salmon were determined in a tunnel-type swimming apparatus during the period from September of the hatching year until May of the following year.

2. Performance was evaluated by systematically increasing water velocity until each fish in a sample of 10 had fatigued.

3. Critical swimming speeds were calculated as estimates of maximum sustainable swimming speeds. Their measures were obtained graphically from probit plots of median swimming performance, on the assumption that the logarithm of fatigue velocity followed a normal distribution.

4. Regression surfaces were calculated relating critical swimming speeds to acclimation and acute (test) temperature experience. Regression surfaces were fitted by response surface analysis, using a non-linear second degree polynomial as a model.

5. The test fish were exposed to normal day-length. Repetition of the experimental design indicated that performance of the coho changed seasonally. The changes observed during the spring period appeared to offer survival value to fish encountering rising temperatures.

6. A 3^3 factorial design was used to investigate the effect of size on temperature-dependent swimming performance. A non-linear response surface model fitted to the data indicated that size had a definite effect on performance, although the quantitative relationship had been estimated with low precision. The results suggested that a more precise

measure of the relation between size and acclimation and acute temperature experience would require increased replication, a larger experimental design, and an increased size range for the fish employed.

7. The acclimation, test-temperature surfaces indicated that the coho is able, through acclimation, to perform relatively independently of temperature over a large part of its temperature tolerance zone. Optimal performance (approximately 5.8 lengths/second) occurred near test and acclimation temperatures of 20° C. Swimming performances for 7.7 cm. to 9.3 cm. coho are of the following order:

Acclimation temp. (° C)	Critical swimming speed (L/sec) at test temperatures			
	5°C	Max. perf. temp.		20°C
5	3.7	5.2	(17.3°C)	4.8
10	3.6	5.5	(18.2°C)	5.3
15	3.4	5.6	(19.0°C)	5.6
20	2.7	5.8	(20.0°C)	5.8

8. The response surfaces suggested that the best performance at a given temperature may not be obtained from fish acclimated to that temperature. This appeared to be the result of a progressive change in the interaction of acclimation temperatures and test temperatures over the performance surface.

9. A change in the nature of the acclimation process was apparent at low temperatures. It was suggested that the decrease in performance noted at low temperatures may be related to the overwintering process. observed for stream-dwelling coho.

10. Precht's adaptation types and Prosser's acclimation patterns were reviewed by considering them as examples of transects across response surfaces. The classifications advanced by those authors were shown to be dependent upon the nature of the surface investigated and the temperature levels of the transects selected.

11. Comparison of temperature-dependent swimming performance for coho and sockeye juveniles suggests that the coho may be better able to perform in warm habitats. The coho possessed a higher temperature optimum than the sockeye, and a greater ability to perform near or slightly above the upper temperature tolerance boundary.

12. A ridge of maximal performance was observed for the coho response surface. On the basis of data available for other species, it is suggested that preferred temperatures for coho may be related to the swimming performance ridge.

13. The hypothesis is advanced that a physiological temperature optimum for the coho, with respect to performance, metabolic scope, growth on excess rations and temperature preference may occur at acclimation and test temperatures near 20°C.

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Appendix I. Data for test series 1

Temperature (°C)		Velocity		Mean size (cm)
AT	TT	L/second	cm/second	
2	2	2.71	19.40	7.17
2	2	3.10	26.55	8.57
2	5	3.75	28.10	7.43
2	8	4.55	34.70	7.62
2	11	4.82	35.90	7.45
2	14	4.60	35.40	7.68
2	17	4.72	35.75	7.57
2	20	4.64	35.70	7.70
5	2	3.33	24.70	7.41
5	5	3.53	26.19	7.41
5	5	3.67	32.25	8.80
5	8	4.19	31.59	7.54
5	11	4.50	33.81	7.51
5	14	4.86	36.40	7.48
5	17	5.00	37.62	7.52
5	20	4.86	36.49	7.50
5	23	1.73	10.67	7.46
8	2	2.94	22.18	7.53
8	5	3.69	28.00	7.59
8	8	4.32	32.58	7.53
8	8	4.17	33.70	8.08
8	11	4.71	35.40	7.52
8	14	4.68	35.35	7.55
8	17	5.29	39.70	7.51
8	20	5.08	38.80	7.64
8	23	4.53	34.58	7.63
11	2	2.88	21.19	7.35
11	5	3.45	25.95	7.52
11	8	4.19	31.19	7.44
11	11	4.46	33.35	7.48
11	11	4.69	37.25	7.94
11	14	5.15	38.75	7.52
11	17	4.87	36.20	7.41
11	20	5.14	39.30	7.64
11	23	5.42	40.45	7.47
14	2	2.95	23.20	7.86
14	5	3.82	29.25	7.67
14	8	4.34	33.80	7.79
14	11	5.04	39.08	7.72
14	14	5.25	41.80	7.97
14	14	5.01	40.40	8.06
14	17	5.58	42.55	7.62
14	20	5.95	46.80	7.86
14	23	5.22	40.55	7.77
17	2	2.67	21.90	8.21

Appendix I (Cont'd.).

Temperature (°C)		Velocity		Mean size (cm)
AT	TT	L/second	cm/second	
17	5	3.36	28.02	8.35
17	8	4.20	36.35	8.65
17	11	4.57	39.90	8.73
17	14	5.12	42.75	8.36
17	17	5.30	46.20	8.71
17	20	5.48	47.10	8.60
17	23	5.82	49.90	8.59
17	26	1.39	11.76	8.46
20	2	0.87	7.09	8.12
20	5	2.89	23.00	7.96
20	8	3.45	27.80	8.06
20	11	4.34	34.90	8.05
20	14	5.02	39.40	7.84
20	17	5.38	41.75	7.76
20	20	6.34	47.00	7.42
20	23	5.64	45.20	8.02
20	26	3.83	30.45	7.96
23	5	1.23	9.20	7.47
23	8	3.38	25.40	7.51
23	11	4.17	31.20	7.47
23	14	4.56	35.12	7.70
23	17	5.29	39.60	7.49
23	20	5.58	41.50	7.44
23	23	5.44	40.80	7.50
23	26	4.42	33.90	7.67
23	27.5	0.72	5.40	7.47

Appendix II. Data for test series 2.

Temperature (°C)		Velocity		Mean size (cm)
AT	TT	L/second	cm/second	
2	2	2.22	20.00	9.01
2	5	3.74	35.20	9.42
2	8	4.29	40.60	9.46
2	11	4.77	45.25	9.50
2	14	4.74	45.20	9.53
2	17	4.85	45.90	9.47
2	20	4.29	40.40	9.41
5	2	1.93	17.40	9.02
5	5	3.49	32.40	9.29
5	8	3.90	36.20	9.28
5	11	4.15	39.15	9.43
5	14	5.04	46.80	9.29
5	17	5.15	48.10	9.35
5	20	5.40	50.30	9.32
5	23	1.28	12.00	9.36
8	2	3.23	28.50	8.82
8	5	3.01	26.60	8.83
8	8	4.52	40.40	8.95
8	11	4.44	43.80	8.95
8	14	5.45	48.40	8.88
8	17	5.53	49.30	8.92
8	20	5.21	46.80	8.98
8	23	5.01	45.15	9.02
11	2	3.18	29.50	9.29
11	5	3.27	30.40	9.30
11	8	4.50	40.70	9.04
11	11	4.54	41.20	9.07
11	14	5.55	51.30	9.24
11	17	5.42	50.40	9.30
11	20	6.02	56.10	9.33
11	23	5.58	51.00	9.14
14	2	3.00	28.00	9.34
14	5	3.49	31.75	9.09
14	8	4.45	41.30	9.27
14	11	4.96	45.80	9.23
14	14	5.28	48.80	9.25
14	17	5.29	49.20	9.29
14	20	5.51	52.00	9.45
14	23	5.25	48.40	9.22
17	2	2.40	23.60	9.84
17	5	3.12	30.60	9.82
17	8	3.68	34.60	9.39
17	11	4.55	45.10	9.92
17	14	4.22	40.10	9.50
17	17	5.09	48.20	9.47

Appendix II. (Cont'd).

Temperature (°C)		Velocity		Mean size (cm)
AT	TT	L/second	cm/second	
17	20	5.11	49.80	9.74
17	23	5.55	54.00	9.73
17	26	1.93	18.50	9.57
20	5	3.28	30.50	9.31
20	8	3.16	29.20	9.23
20	11	4.40	40.30	9.17
20	14	5.28	48.25	9.14
20	17	5.49	49.40	9.00
20	20	5.69	51.80	9.10
20	23	6.04	54.20	8.98
20	26	3.88	34.45	9.13
23	5	1.40	13.00	9.32
23	8	3.29	31.08	9.44
23	11	4.66	44.20	9.48
23	14	4.98	47.10	9.46
23	17	5.29	50.00	9.46
23	20	5.52	52.40	9.50
23	23	5.32	50.30	9.45
23	26	3.93	36.99	9.41

Appendix III. Data for test series 3.

Temperature (°C)		Velocity		Mean size (cm)
AT	TT	L/second	cm/second	
5	23	1.48	10.40	7.01
5	23	1.46	13.00	8.90
5	23	1.38	14.70	10.62
5	14	5.18	36.80	7.11
5	14	5.30	45.80	8.64
5	14	4.46	48.30	10.83
5	5	3.87	27.00	6.98
5	5	4.11	35.40	8.61
5	5	3.49	37.55	10.77
14	23	5.56	39.90	7.17
14	23	5.53	49.90	9.02
14	23	5.18	55.70	10.75
14	14	5.33	39.80	7.47
14	14	5.38	49.10	9.13
14	14	4.39	48.70	11.09
14	5	3.88	28.10	7.24
14	5	3.21	28.75	8.97
14	5	3.70	41.00	11.08
23	23	4.77	34.35	7.20
23	23	5.35	48.70	9.10
23	23	5.12	57.40	11.21
23	14	4.48	32.60	7.30
23	14	4.76	43.30	9.10
23	14	4.33	47.40	10.95
23	5	2.83	21.10	7.47
23	5	3.23	29.80	9.22
23	5	2.35	25.25	10.75

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