EFFECTS OF SALINITY AND TEMPERATURE ACTING IN CONCERT ON SUSTAINED SWIMMING SPEED OF JUVENILE COHO SALMON (ONCORHYNCHUS KISUTCH)

by

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ABSTRACT

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The effects of salinity (freshwater - 20 ‰) and temperature (3-23C) acting in concert on sustained swimming speed of juvenile coho salmon (4.9-11.4 cm) acclimated to test conditions were examined in a stamina tunnel. Relations between swimming performance and test parameters were examined by response surface analysis, employing a second order polynomial as a model.

Sustained swimming speed of coho fry - presmolt developmental stages declined with decreasing temperatures from about 20 C, but were little affected by salinities ranging from freshwater to 20 ‰S. In the smolt stage, temperature effects were similar but salinity effects more pronounced, with maximum levels of performance attained at near isotonic salinities. Optimum locomotor capacity occurred at about 20C in all developmental stages tested, ranging from 7.2 Lengths/second (L/sec) in fry to 5.5 L/sec in smolts. Relative swimming capacity was size dependent, and the extent of this dependence was related to temperature. With decreasing temperatures, smaller fish showed a greater decrease in relative swimming capacity. At 3C, size effects on relative capacity were virtually nonexistent and all test stages attained a performance of about 3.5 L/sec.

The results suggest that underyearling coho have the capacity to perform locomotor-dependent behaviours in brackish waters, up to a salinity of at least 20 ‰, with an efficiency equivalent to that in freshwater.

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INTRODUCTION

Temperature and salinity are important physical factors of the aquatic environment. Major contributions towards an understanding of temperature effects on the activity of fish were made by Fry (1947, 1964, 1967) and Brett (1964, 1965, 1967), whereas knowledge on the influence of salinity is somewhat limited (Rao, 1968, 1969; Farmer and Beamish, 1969). More recently, Griffiths and Alderdice (1972) investigated the effects of acclimation and acute temperature experience on the swimming capacity of juvenile coho salmon (*Oncorhynchus kisutch*, Walbaum). This species is the subject of the present study.

The conventional life history pattern of this Pacific salmon is one in which a year of stream residence precedes a well defined period of smoltification and seaward migration. However, in some coho populations, a majority migrate to sea as fry (Chapman, 1962) and this movement appears to be the result of intraspecific competition for food and space (Mason and Chapman, 1965). Associated with such migrations is the question of the coho's ability to survive entry into the ocean, and to perform activities essential to continued survival, prior to the conventionally accepted time of seaward migration as yearling smolts.

Coho underyearlings are believed to be poorly equipped physiologically and behaviourally for life at sea (Black, 1951; Hoar, 1958). Arrayed against this notion is considerable evidence to suggest that underyearling coho have the physiological capacity to perform as well in seawater as in freshwater, provided the transition is gradual (Otto, 1971). Conte et al (1966) have shown that underyearling coho are able to meet the problems of osmotic and ionic regulation in seawater if given an opportunity to acclimate. Under laboratory conditions, growth in seawater more concentrated than isotonic levels has been reported comparable to that obtained under freshwater conditions (Canagratnam, 1959; Otto, 1971). On the other hand, authenticated records of sea growth in 0-year class coho are very limited (Pritchard, 1940; Milne, 1962). More than 95% of the coho fishery consists of fish that entered the sea in the 2-year class (Godfrey, 1965). The fate of the large numbers of coho presmolt emigrants is currently unknown, but presumably their almost complete loss is not the result of physiological limitations.

One other possibility for investigation is that of sustained swimming performance of juvenile coho over their ranges of salinity and temperature tolerance. Conceivably, such measurements would reflect the young animal's ability to conduct behaviours dependent on locomotion such as food capture, predator avoidance and migratory movements. The present study describes the effects of salinity and temperature acting in concert on sustained swimming speeds of coho, from fry to smolt stages, with some reflection on size effects. The ability of young coho to survive early entry into the sea is assessed in the light of their swimming capacity to salinity and temperature.

MATERIALS AND METHODS

Source and Culture of Fish

Coho salmon were collected as fry from Cook Creek, Vancouver Island, British Columbia, and transferred to outdoor holding tanks at the Biological Station, Nanaimo, British Columbia. Tests of swimming performance on the full range of premigratory developmental stages necessitated the collection of fish from two different year classes. Fish used in tests on advanced fry to smolt stages were captured between July 2 and August 20, 1970; tests on fry utilized fish collected between July 2 and August 27, 1971.

Fish stocks held outdoors were exposed to seasonal changes in photoperiod and ambient fresh water temperatures (Fig. 1). Incoming water supply to the tanks provided a velocity of about one fish fork length per second (L/sec). The fish initially were fed frozen brine shrimp (Artemia spp.) until accustomed to artificial feeding, followed by a diet of pelleted food (Abernathay formula) fed twice daily, six days per week.

Determination of Salinity Acclimation

Rates of acclimation of juvenile salmonids to salinity are not well documented. Prior to tests on swimming performance, salinity survival experiments were conducted (August 27 - October 31, 1970) to determine acclimation rates to salinity at constant and changing temperatures.

Fish from the outdoor stock were anaesthetized in tricaine methanesulphonate (MS-222) at an approximate concentration of 100 ppm and sorted to provide samples of uniform size (mean fork length ± 1 SD).

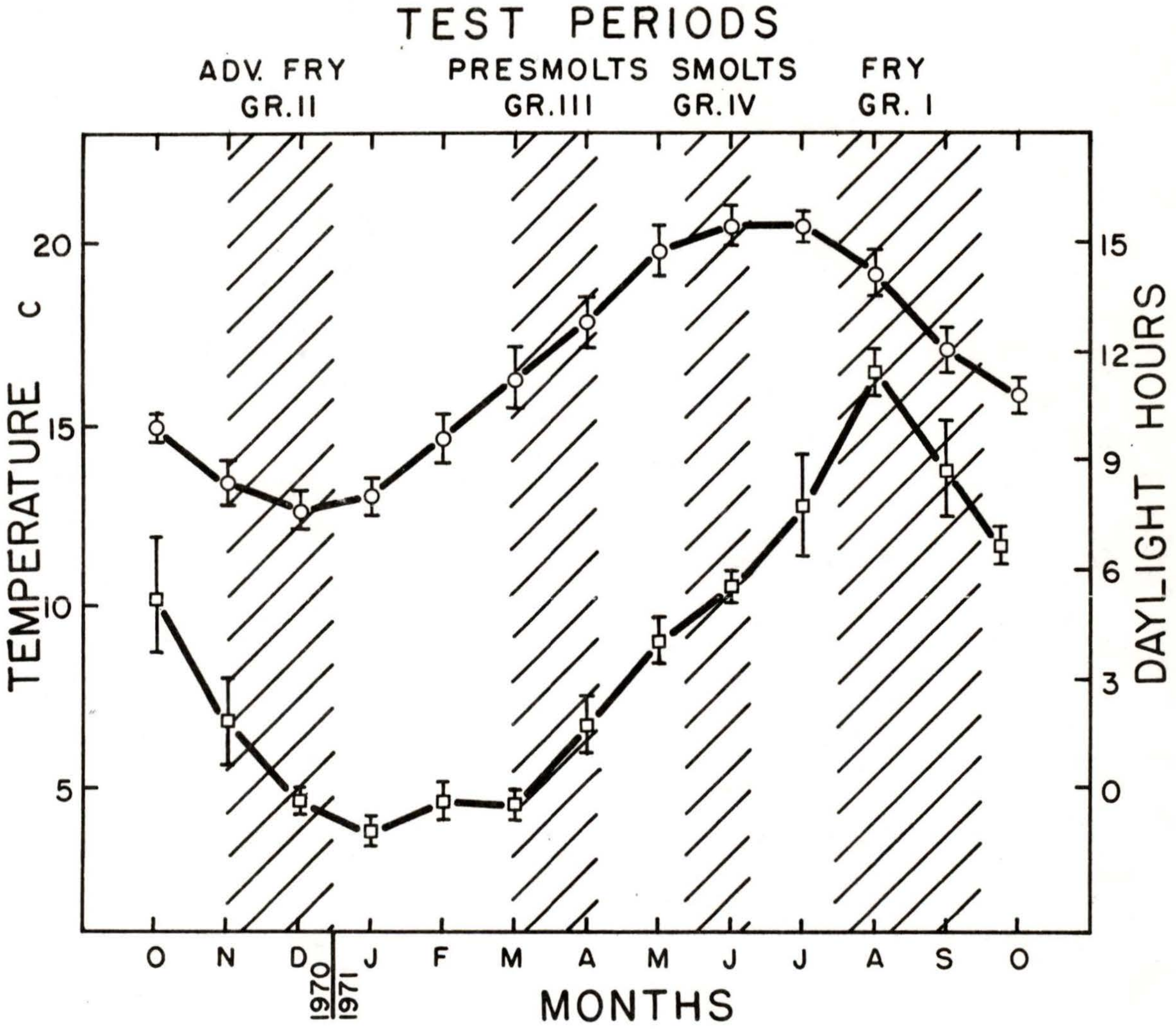

FIG. 1. Seasonal changes in ambient freshwater temperature (□) and acclimation facility photoperiod (O). Symbols: mean monthly values ± one standard deviation. Test periods are shown as hatched areas. Daylight refers to daily period of artificial illumination in acclimation room, controlled by photo-electric cell exposed to natural photoperiod.

These samples were held indoors for one week in circulating fresh water at the ambient temperature of approximately 16C. Salinity (‰S) was then increased to 15 ‰ within two hours by manual control of the incoming water supply and maintained at 16C.

Changes in survival time were determined for groups of 10 fish at 45 ‰S ± 0.1 and 16C ± 0.1 after 1, 2, 4, 8, 16, 32, and 42 days of exposure to 15 ‰ and 16C (Fig. 2). The lethal test salinity was prepared at least 12 hours in advance by dissolving artificial sea salt (Rila Marine Mix) in sea water in 35L insulated fiberglass tanks. With continuing exposure to the hypersaline medium, fish exhibited loss of equilibrium, buoyancy problems, and an increase in ventilation rate. Fish were considered dead when no opercular acticity was detected within two minutes. Throughout the experimental period fish were fed twice daily a diet identical to that provided to the outdoor stock, and deprived of food a minimum of 12 hours prior to testing.

Median survival times for each test group were obtained in linear plots of logarithms of survival time (in minutes) against cumulative per cent mortality on a probit scale. The relation between median survival times and days of exposure to 15 ‰S indicated that maximum survival time at 45 ‰ was attained within eight days (Fig. 2). Physiological adjustment to salinity in underyearling coho appears to occur at a rate of about 2 ‰ per day at 16C.

Additional survival tests were conducted to determine if acclimation rates of 2 ‰S and 1C per day would be maintained in concert. Changes in survival time were determined at 45 ‰S ± 0.1 and 16C ± 0.1 among samples taken from freshwater at 5C and held at 15 ‰S and 16C

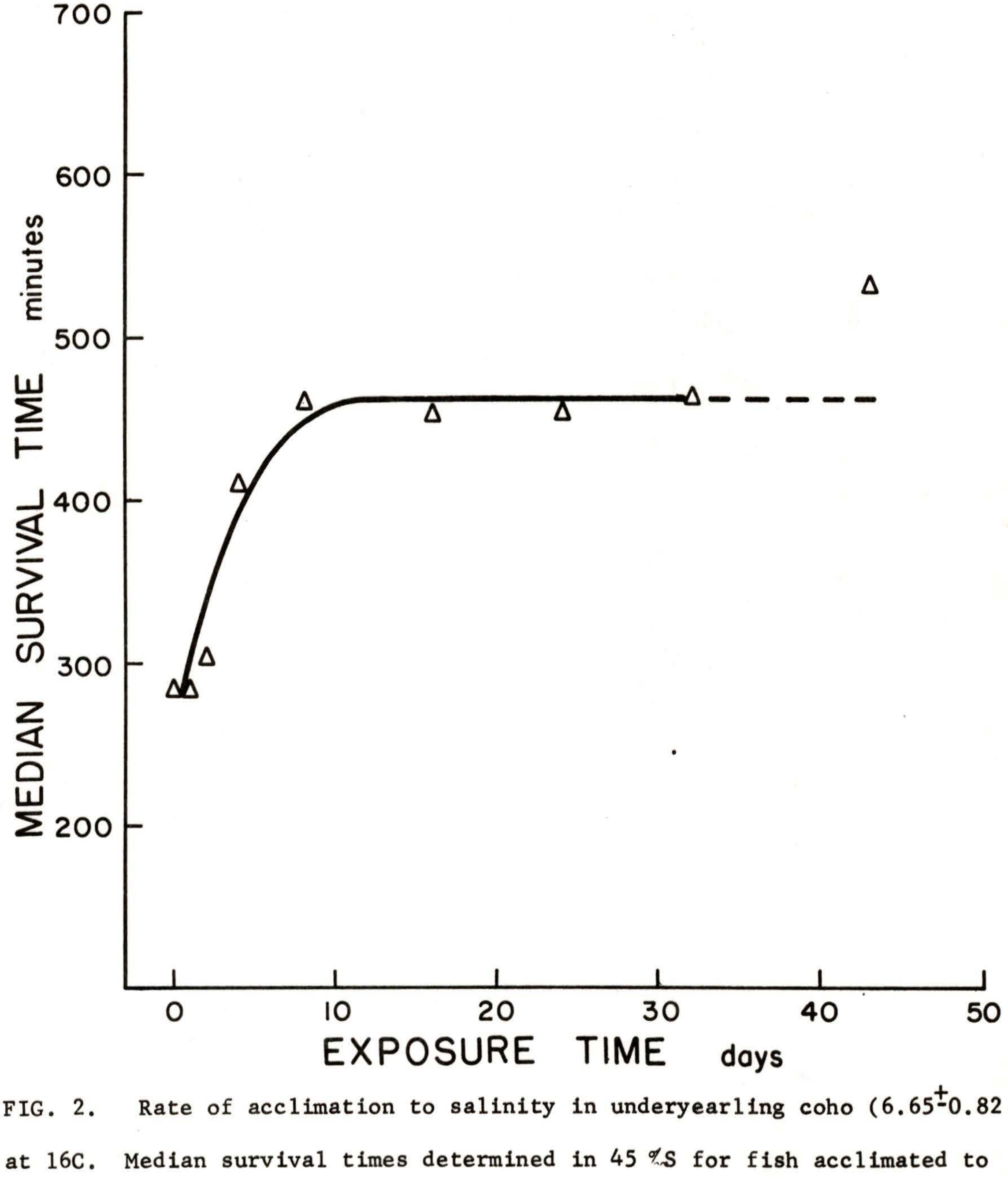

FIG. 2. Rate of acclimation to salinity in underyearling coho (6.65±0.82 cm) at 16C. Median survival times determined in 45 ‰S for fish acclimated to freshwater (16C) and put at 15 ‰S. The high value at 42 days represents sampling bias (mean length 8.06 cm).

for various lengths of time prior to transfer to the lethal salinity (Fig. 3).

Rate of acclimation of juvenile coho to temperature, in fresh water, is not well documented. On the basis of data available for other species (Brett, 1944, 1946), rate of acclimation to temperature appears to depend on metabolic rate, and is determined by the level of temperature to which the fish is acclimated and the direction in which temperature is shifted. On the basis of change in temperature alone, between 5 and 15C, acclimation could be expected to be complete in about 15 days (Brett, 1946). In terms of absolute value, it appears that acclimation to salinity occurs more rapidly than that to temperature (between 5 - 15C). Hence, rate of acclimation to salinity and temperature, changed concurrently, may depend primarily on the response to temperature. In the present case, beyond 15 days of exposure, there was very little change in survival times, supporting the conclusion that acclimation rates to combined temperature and salinity changes are similar to the rates obtained for temperature changes alone. On this basis, minimum acclimation periods equivalent to a change of 1C per day are considered reasonable over the temperature range (3-23C) considered.

Swimming performance of juvenile coho was used to verify acclimation rates of 2 ‰S and 1C per day. All fish were tested at the extreme combination of 20 ‰S and 23C. Samples taken from freshwater at 6C were tested at 2 day intervals of acclimation to accumulative increments of 5 ‰S and 2C until the combination of 20 ‰ and 14C was reached. Beyond this point, tests were conducted at less frequent

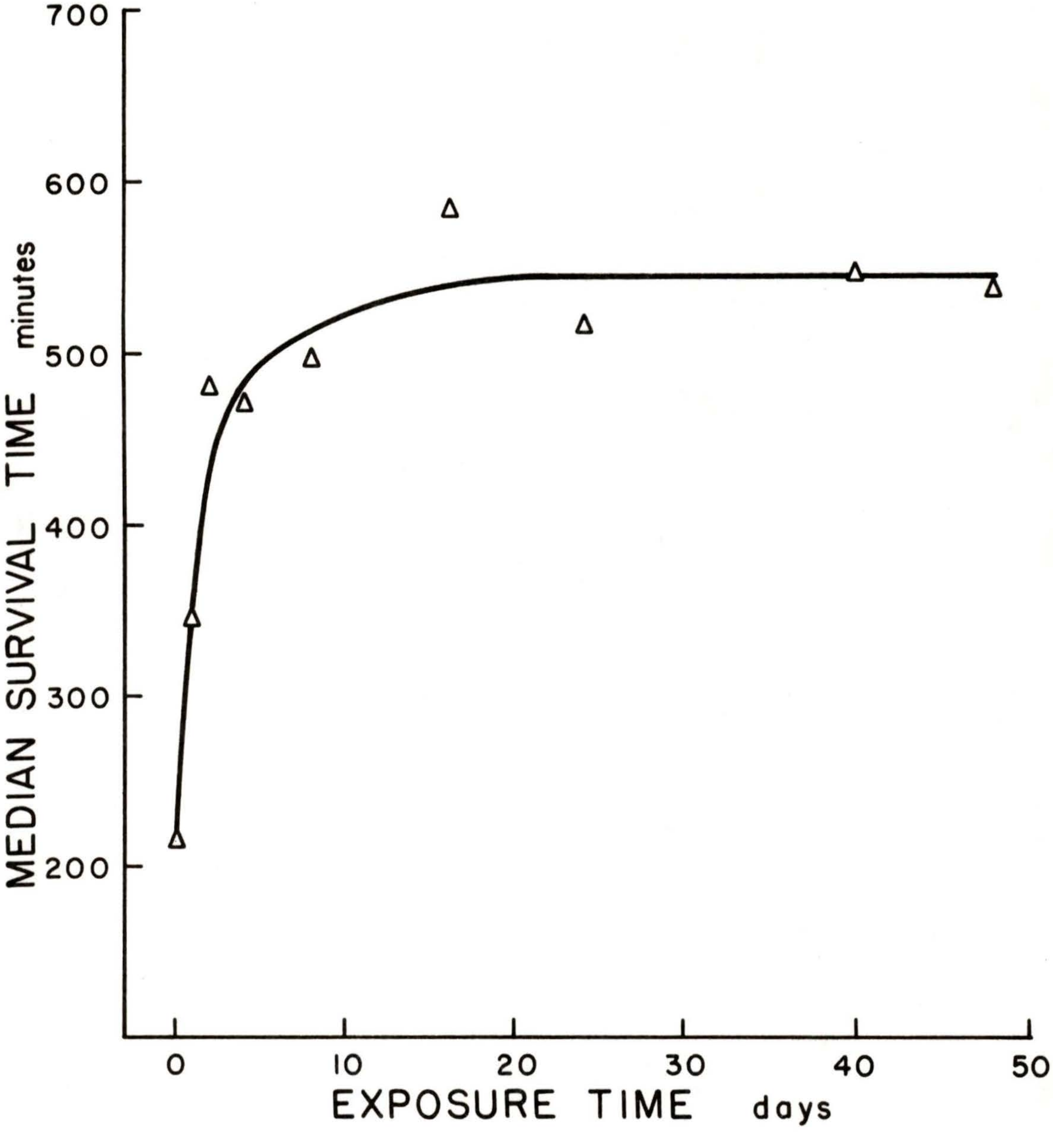

FIG. 3. Rate of acclimation to salinity and temperature acting in concert, for underyearling coho (7.29±0.87 cm). Median survival times determined in 45 ‰S at 16C, for fish acclimated to freshwater at 5C and put at 15 ‰S and 16C.

intervals (Table I). Performance values reached a constant level at acclimation conditions approaching a combination of 20 ‰ and 18C in approximately 15 days (Fig. 4), suggesting that incremental rates of increase in salinity and temperature imposed (1C and 2.5 ‰/day) were within the animal's acclimation capacity.

Acclimation Facilities

Ten 80L insulated fiberglass tanks (Alderdice et al, 1966) were used for acclimation of the juvenile coho. Each tank was provided with thermostatically controlled heater, aeration, and continuous recirculation (Figs. 5, 6). Five tanks were also equipped with thermostatically controlled circulation of chilled ethylene glycol through cooling coils for low temperature acclimations. Illumination was provided by overhead fluorescent lamps switched on and off by a photoelectric cell positioned in a north window exposed to natural daylight (see Fig. 1).

Required fresh and salt water supplies for acclimation were gravity-fed and manually controlled from a header system of insulated glass reservoirs suspended from the ceiling (Figs. 5, 6). All incoming water to the header system was filtered (5μ cartridge-type cellulose filter) of particulate matter. In addition, all fresh water was shunted through stripping columns and scrubbed of excess gases. Delivery of fresh and salt water into each acclimation tank was regulated through a bank of nylon valves, manifolds and flowmeters, permitting acclimation salinities to be held within ± 0.5 ‰.

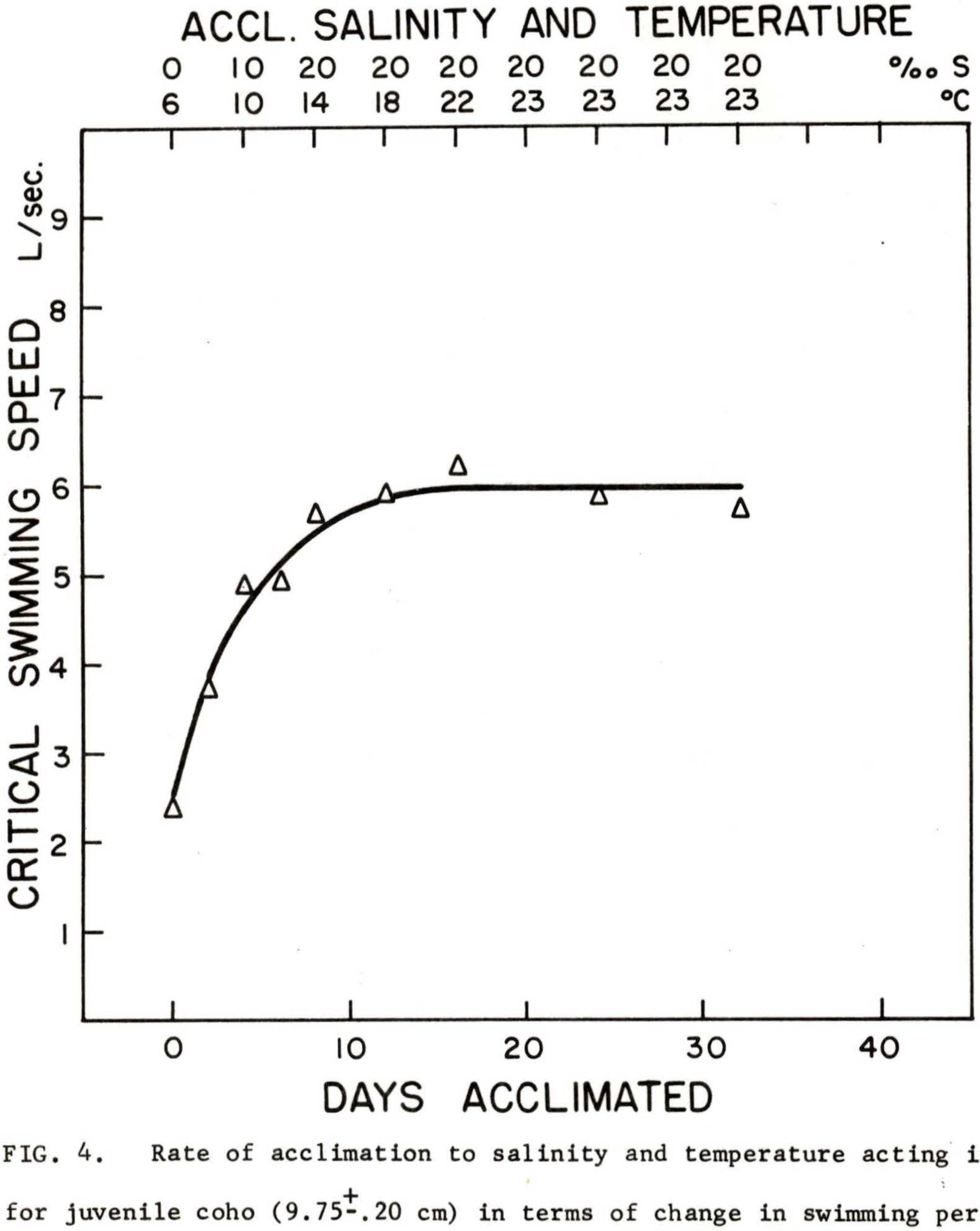

FIG. 4. Rate of acclimation to salinity and temperature acting in concert for juvenile coho (9.75±.20 cm) in terms of change in swimming performance. Critical swimming speeds determined in 20 ‰S at 23C, for fish previously acclimated to freshwater at 6C and tested at the increasing acclimation salinity-temperature combinations indicated.

TABLE I Rate of acclimation to salinity and temperature in concert determined by critical swimming speed of juvenile coho tested at 20 ‰S and 23C.

Days acclimated	Acclimation salinity (‰)	temperature (C)	Critical Swimming Speed (L/sec)
0	0	6	2.18
2	5	8	3.69
4	10	10	4.85
6	15	12	4.90
8	20	14	5.66
12	20	18	5.86
16	20	22	6.18
24	20	23	5.85
32	20	23	5.70

Mean fork length of fish ± 1 SD = 9.76 ± 0.39 cm

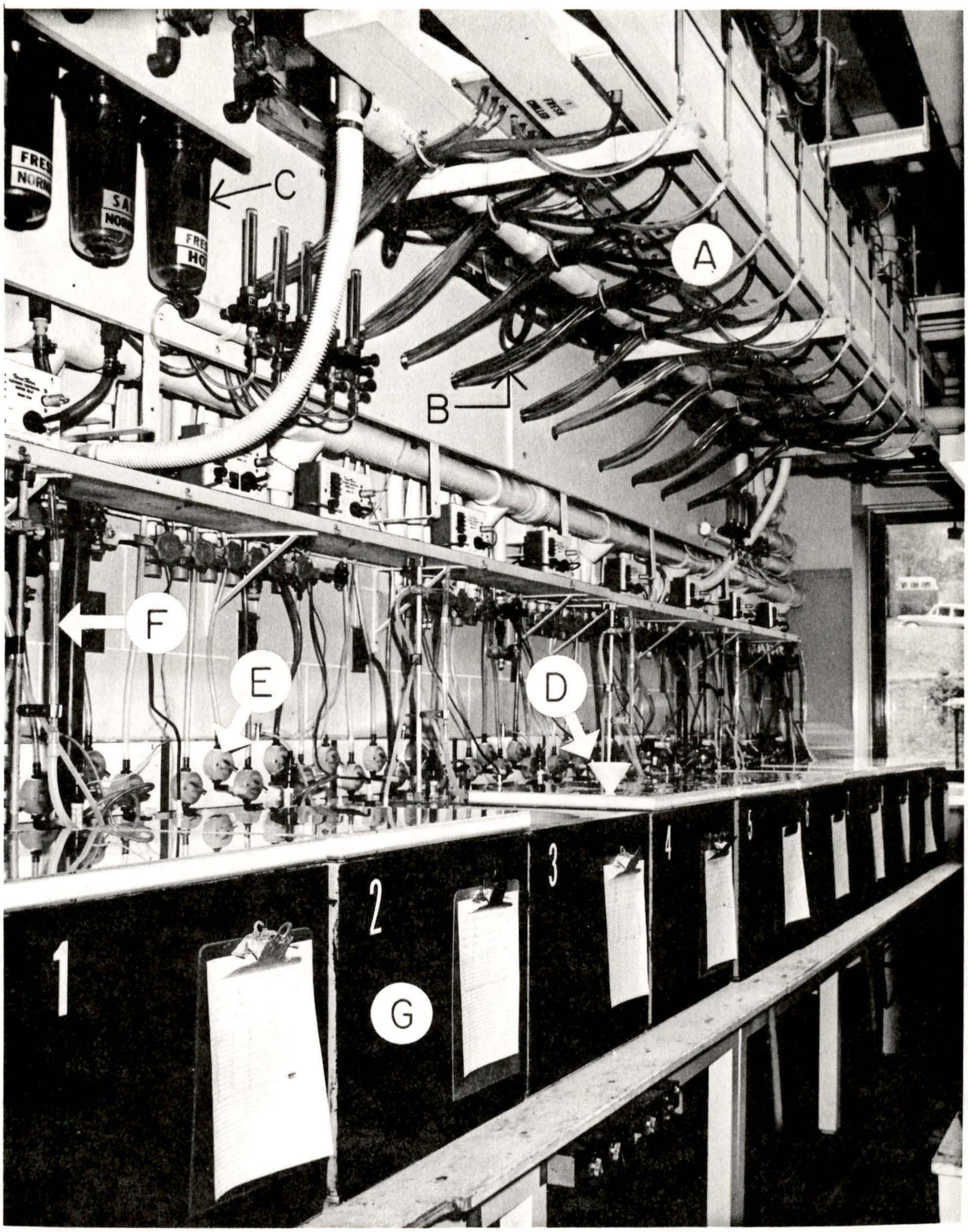

FIG. 5. Photograph of acclimation facilities. A, insulated header-tank system; B, water supply lines to acclimation tanks; C, water filter; D, plastic feeding funnel; E, two-way nylon valve; F, glass flowmeter; G, insulated fiberglass tank.

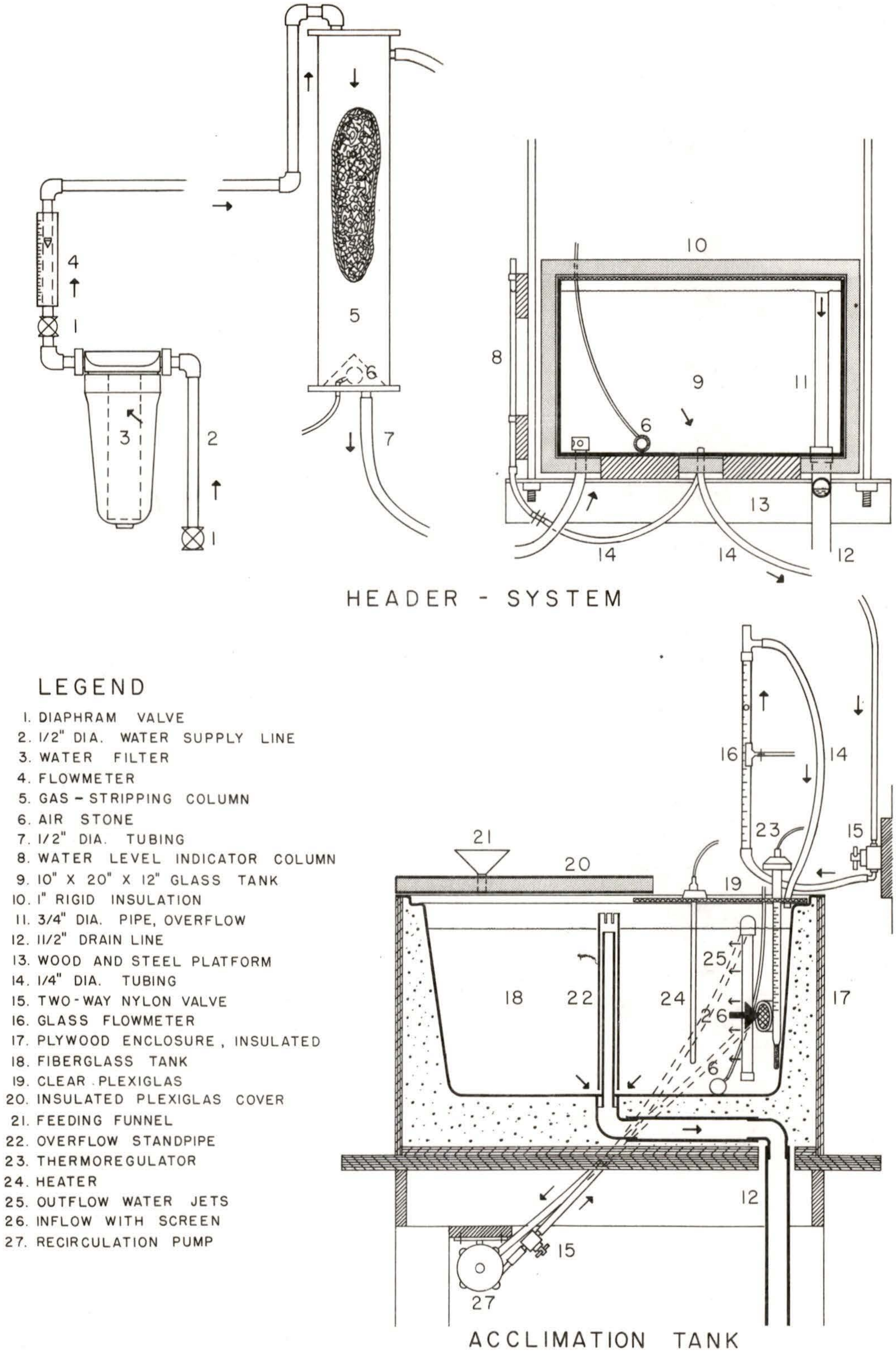

FIG. 6. Diagrammatic illustration of the acclimation facilities. The direction of water flow is indicated by the arrows.

Acclimation Procedure

Fish were transferred indoors from the outdoor holding tank for size selection. To compensate for growth, fish at the beginning of a test series were selected for a fork length slightly greater (about 0.5 cm) than the mean size of the outdoor holding stock. Fork lengths (FL) were used throughout this study on the basis that such measurements were more accurate than total length. Prolonged culture of juvenile salmon usually results in slight damage to posterior margin of caudal fin.

Incoming water to all acclimation tanks was maintained at a flow rate of 30L/hour. The average water velocity was adjusted to one fish length per second using an Ott current meter. This combination provided adequate removal of settled waste material to the tank drains and temperature control within ± 0.1C. The salinity of incoming sea water was measured daily (portable salinometer) to provide a value for calculating the proportional rates of delivery of fresh and salt water to each tank.

Rates of acclimation to salinity and temperature in concert were set at daily increments of 2.5 ‰S and 1.0C, respectively, until the desired test combination was attained. This salinity increment was most convenient since the test salinities occurred in multiples of 2.5. In the case of salinity-temperature combinations only slightly different from the holding conditions, minimum acclimation time was set at one week, to allow the fish to recover from the stress of handling and to resume feeding.

Test Apparatus

The stamina tunnel (Fig. 7) used in this study was that described by Griffiths and Alderdice (1972). The apparatus was equipped with temperature and velocity control. Basically, it consisted of an experimental chamber made of clear acrylic tubing (5 3/4" I.D. x 24" long), linked to a large recovery section and recirculating tunnel constructed of glass fibre reinforced plastic. Water was recirculated by a five-bladed propeller, driven by a constant speed electric motor. At the upstream end of the experimental chamber was a set of stainless steel turbulence screens providing microturbulent flow. An electric barrier situated at the downstream end induced fish to swim until fatigued. A more complete description of the apparatus is provided by Griffiths (MS 1969).

Minor modifications were made to the stamina tunnel in the present study. A Plexiglas entry device (Fig. 8) was constructed to utilize water in the recovery section of the swimming apparatus, since all acclimation and test salinity-temperature combinations were identical. A dimmer switch was connected to the lamp at the downstream end of the experimental chamber to minimize light shock when lights were turned on. The one-way mirror was fitted into a housing to improve the visual isolation of the test chamber. For tests with fry, a finely divided nylon screen (spacing, 0.4cm horiz. x 1.4cm vert.) was placed at the entry to the recovery section to prevent fish from passing through when fatigued. Finally, filters were installed on the incoming fresh and salt water lines to lessen the accumulation of debris on the microturbulence screens at the upstream end of experimental chamber. The

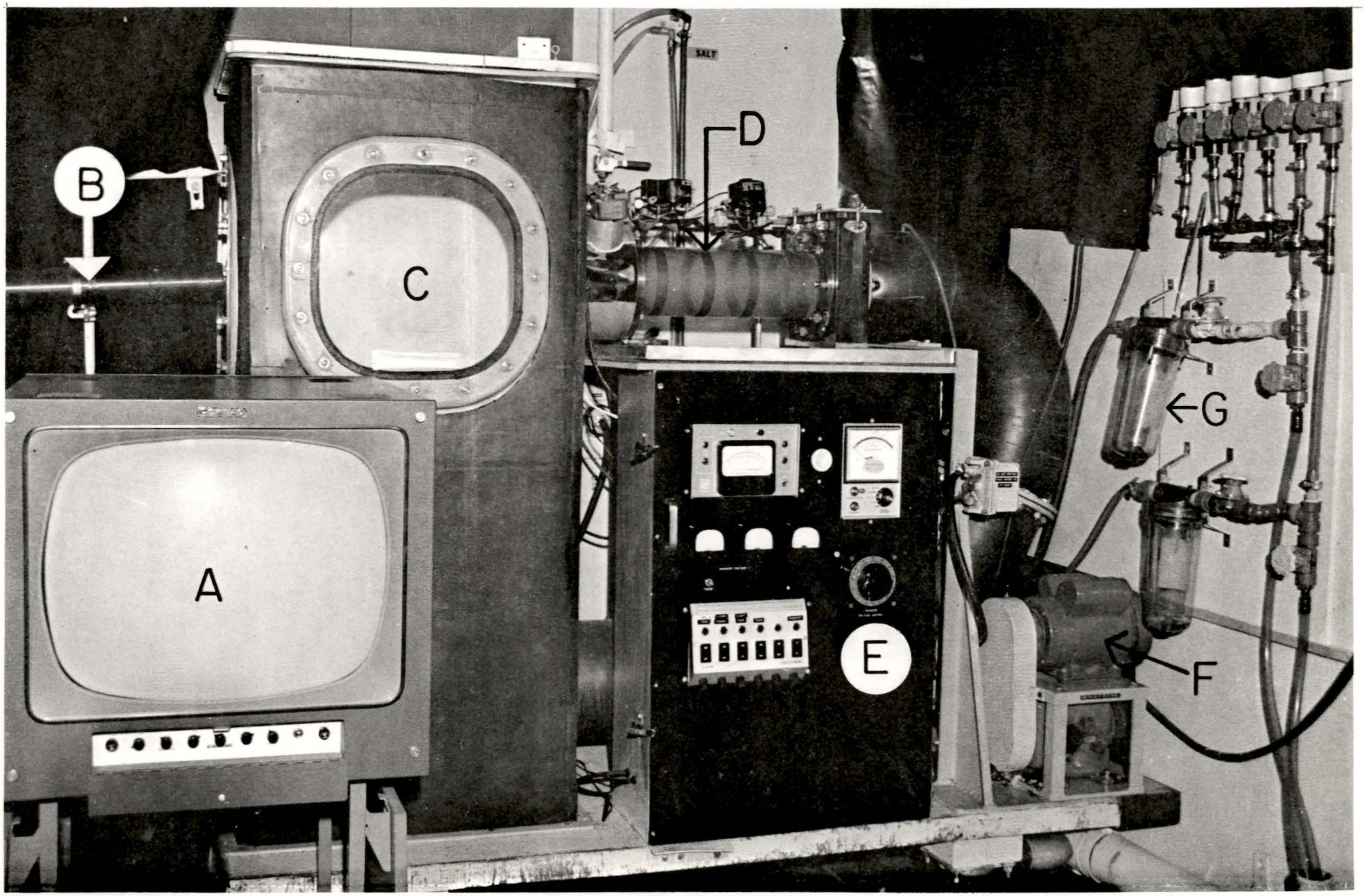

FIG. 7. Photograph of stamina tunnel and accessories. A, television monitor; B, underwater television camera; C, recovery section of stamina tunnel; D, experimental section; E, instrument panel; F, 3/8 H.P. constant-speed electric motor; G, water filter.

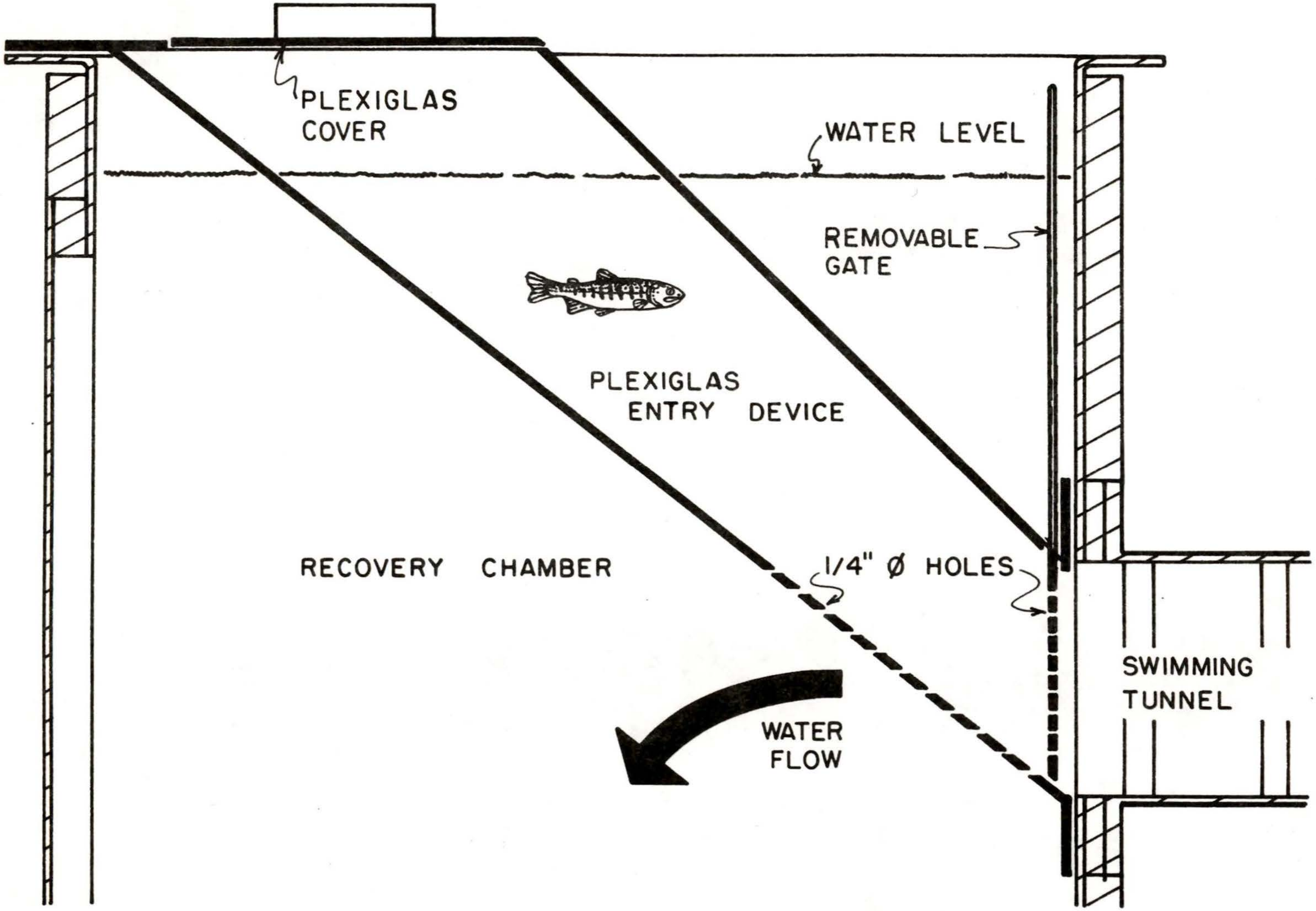

FIG. 8. Removable entry device used to put fish into experimental chamber of stamina tunnel.

entire experimental area was contained within a lightproof enclosure. A television camera and monitor were used to facilitate continuous, remote observation and recording of time-to-fatigue in test fish.

Test Procedure

Test salinities and temperatures ranged from freshwater to 20 ‰S and 3 to 23C, respectively. Critical swimming speeds (Brett, 1964) were examined seasonally (Fig. 1) in random order over a minimum of the 25 salinity-temperature combinations of a 5 x 5 factorial design (Fig. 9). The development stages of juvenile coho salmon tested are designated as follows: fry (Group I, including two fully replicated series), July 29 - October 1, 1971; advanced fry (Group II), November 16- December 30, 1970; presmolts (Group III), March 15 - April 19, 1971; and smolts (Group IV), May 27 - June 23, 1971. Towards the end of the presmolt test series, some fish were beginning to show signs of smoltification, characterized by less distinctly visible parr marks and silvery coloration on the sides. All of the smolts (Group IV) tested revealed the signs of smoltification described by Garison (1965). The period of coho smolt emigration in Cook Creek and adjacent areas of Eastern Vancouver Island has been observed to occur from early April through May (P. Wickett, unpublished data).

Test salinities in the swimming speed apparatus were established to within ± 0.1 ‰ by mixing appropriate amounts of fresh and salt water. The apparatus was then set at a low velocity for a minimum of 12 hours prior to testing, to allow for equilibration of dissolved oxygen and stabilization of test temperature (± 0.1C). Aeration of the test medium was regulated by a flowmeter and dissolved oxygen was checked

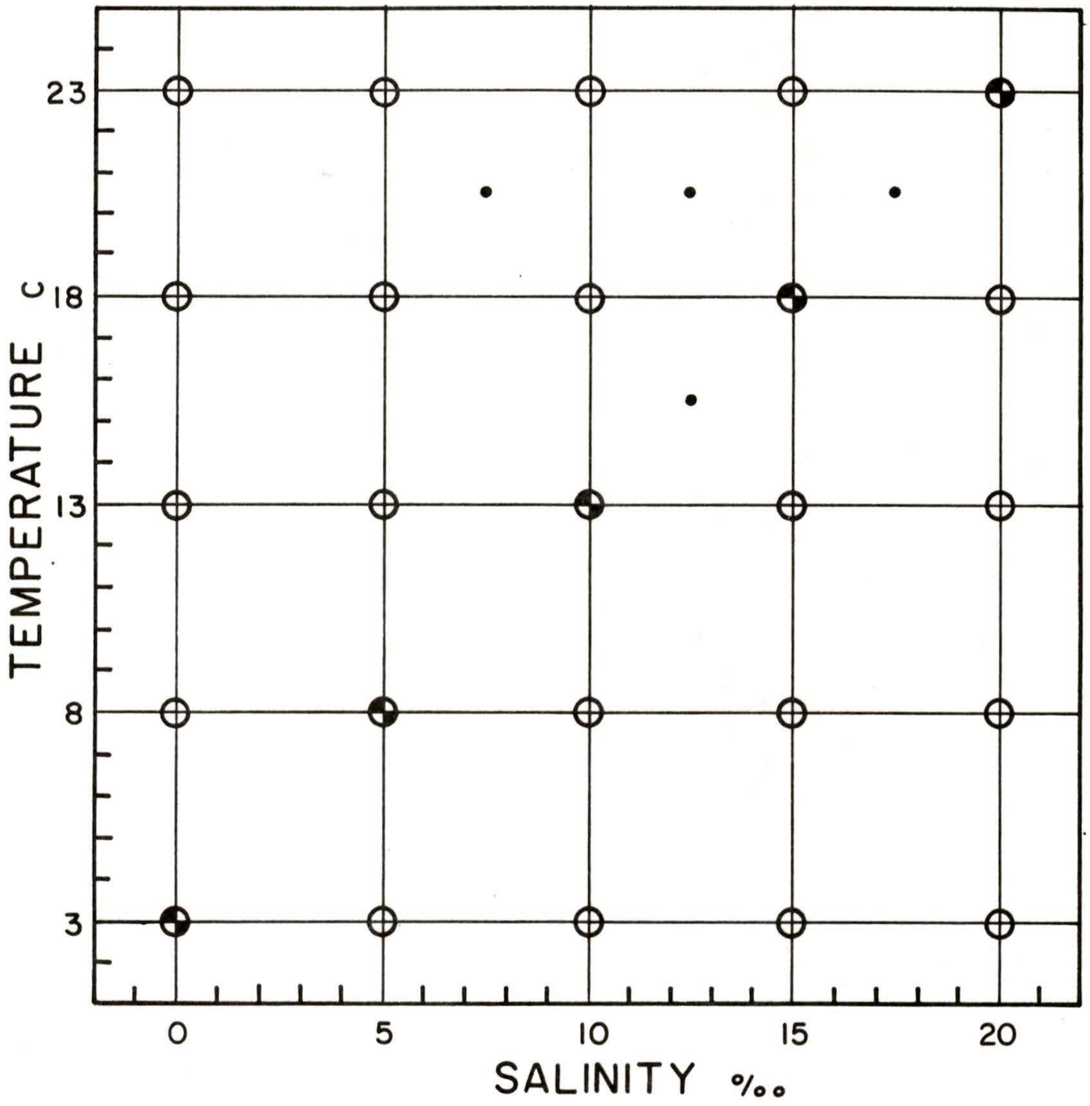

FIG. 9. Salinity-temperature acclimations at which critical swimming speeds were examined. To those of the basic 5x5 factorial design (⊕, ◕) were added 4 additional acclimations (•) in the advanced fry and presmolt stages. Acclimations on the salinity-temperature diagonal (◕) are discussed in the text.

periodically with an oxygen meter to ensure that all performance tests were conducted at near saturation levels.

For each test, ten acclimated fish were transferred in semi-darkness into the entry device, with the test apparatus operating at a velocity of one fish length per second, the same as the acclimation tank velocity. An overhead fluorescent lamp in the recovery section was switched on after five minutes, stimulating the fish to move into the dimly illuminated experimental chamber. The entry device was then replaced by the nylon screen and the lamp at the rear of the experimental chamber gradually brought to full light intensity. The electric barrier was initially set at a low voltage and was increased by hourly increments to about 6 volts. Following transfer to the test section of the stamina tunnel, fish were allowed one hour to recover from handling and to adjust to the apparatus. To check the adequacy of the one-hour recovery period, tests were also conducted on fish introduced into the test section of the stamina tunnel twelve hours prior to testing (Table II). No significant difference was found in swimming performance.

The relation between water velocity in the experimental section and propeller shaft rotation was established weekly with an Ott current meter. The water velocity in the stamina tunnel was increased incrementally throughout the experiments in a manner similar to that developed by Brett (1964). Velocity increments approximately one-eighth the maximum swimming speed at each test temperature (estimated from Griffiths, MS 1969) were applied at one-hour intervals. Fish would generally fatigue after 7 to 10 hours of swimming. Critical velocities

TABLE II Critical swimming speeds (L/sec) for coho fry allowed different periods of recovery time following transfer into stamina tunnel.

	1 hour	12 hours
	7.18	7.00
	7.08	6.70
Mean	7.13	6.85
ts =	0.84 ns	

were estimated by interpolation (Brett, 1964) in cases where fish did not fatigue exactly at the beginning or end of an hourly velocity increase. Median critical swimming speeds were obtained from probit plots of the individual speeds attained in each test sample.

Fatigued fish were anaesthetized, weighed, measured (Fig. 10) and returned to their acclimation tank as a check on post-fatigue mortality. The following day they were transferred to an outdoor holding tank. The numbers of smolts (Group IV) with no previous exposure to the test apparatus (naive) were limited; about 80% of the test animals in that group were fish that had been tested in the advanced fry (Group II) series, four months previously. All other test groups used naive fish only.

Replicate tests for advanced fry-smolt stages (Groups II-IV) were conducted within the same test period at combinations in the factorial space where performance estimates deviated appreciably from adjacent values (about 15% of the test combinations). In such cases the mean value was entered in the data analysis.

Comparison with Coho and Sockeye

To provide a brief comparison with coho, performance tests on sockeye were conducted on acclimated presmolts and smolts, for the salinity-temperature combinations along the diagonal of the factorial space (see Fig. 9). These fish were incubated, hatched, and cultured indoors at the Biological Station, Nanaimo, British Columbia, and fed a diet similar to the coho test stock. All experimental procedures used were similar to those previously described.

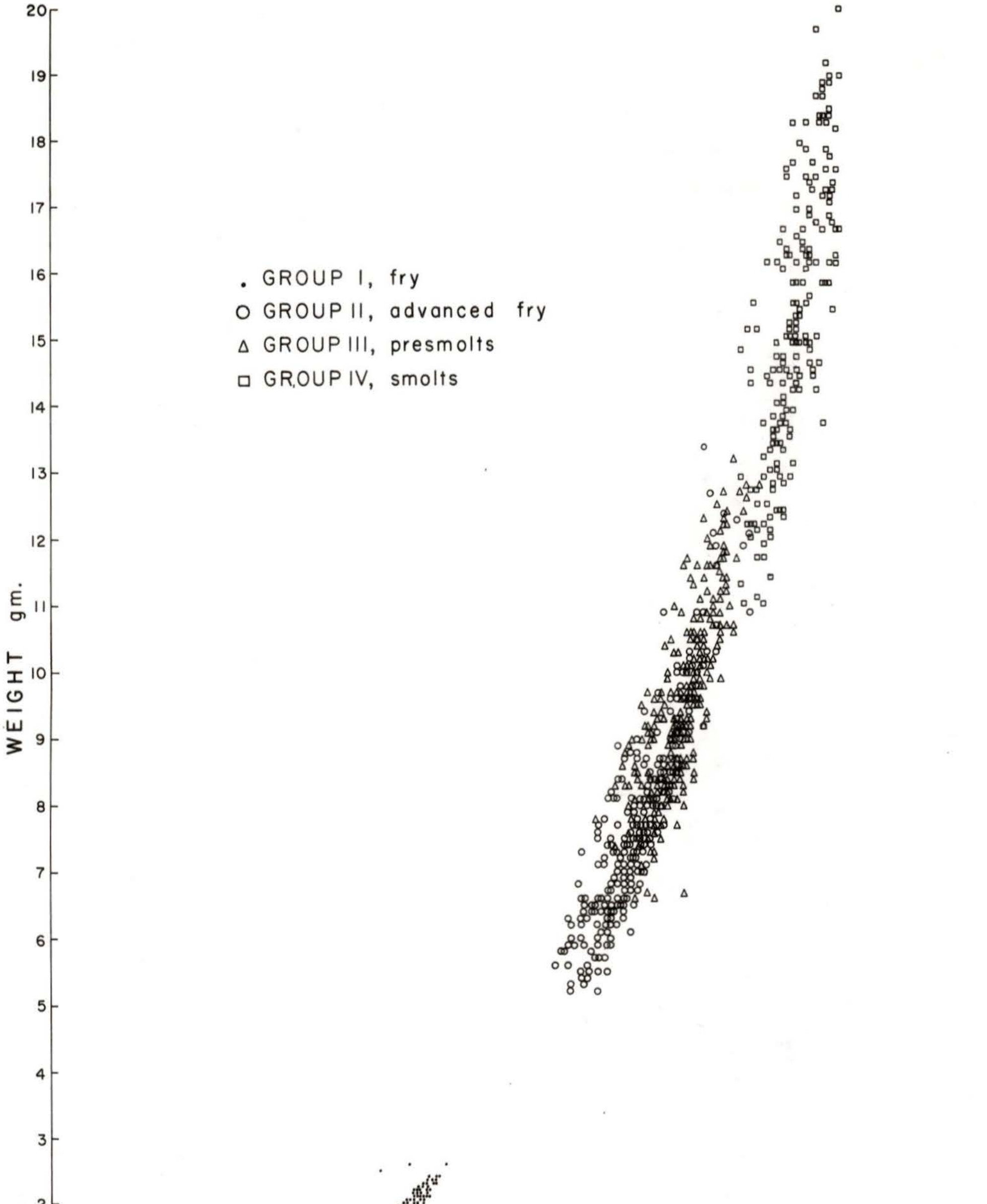

FIG. 10. The chronological relationship of wet weight to fork-length of the juvenile coho salmon used in the swimming performance tests.

In addition, the performance of coho and sockeye advanced fry acclimated in freshwater at 3.5C was determined for the salinity-temperature combinations along the diagonal of the factorial space; the intent was to obtain an appreciation of the swimming capacities for both species when tested acutely at increasing salinity-temperature combinations.

Possible Factors Influencing Variability in Performance

Substantial heterogeneity in the swimming performance of individual fish from wild populations might be expected because of genetic variability. Degree and type of parasitic infection could also contribute to variation in swimming performance of fish. Butler and Milleman (1971) have shown that the salmon poisoning trematode, Nanophyetus salmincola, can markedly impair the swimming ability of underyearling coho and steelhead trout. In this study, the role of behavioural interactions on group performance was considered.

A. Influence of test sample size on performance

Throughout the test, agonistic behaviour was most prominent in Group IV (smolts). Tests were conducted with coho post-smolts during July 2 - 21, 1971, to examine the influence of aggressive behaviour on swimming ability by varying the numbers of fish included in a test group. Under routine procedures, the fish were acclimated and tested in the stamina tunnel at 10 ‰S and 13C, using 1, 5, and 10 fish per test (Fig. 11). No significant difference in performance was noted between group means (Table III).

Much of the repertoire of juvenile coho agonistic behaviour des-

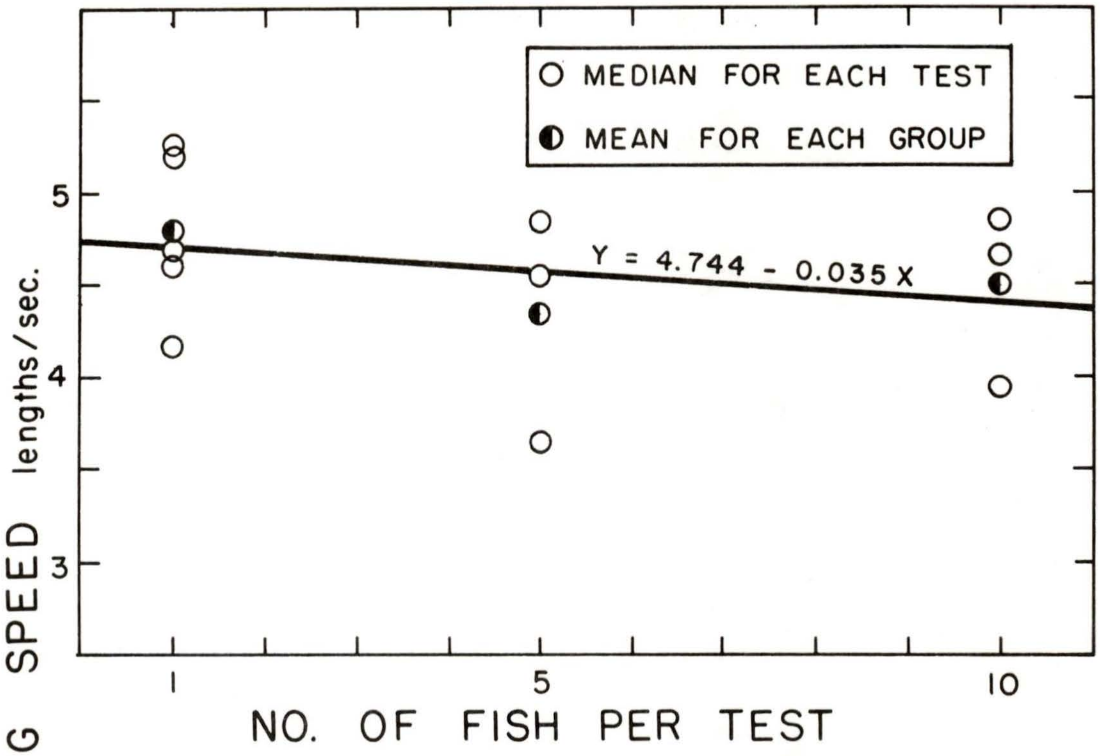

FIG. 11. Effect of sample size on measured swimming performance of coho postsmolts at 10 ‰S and 13C.

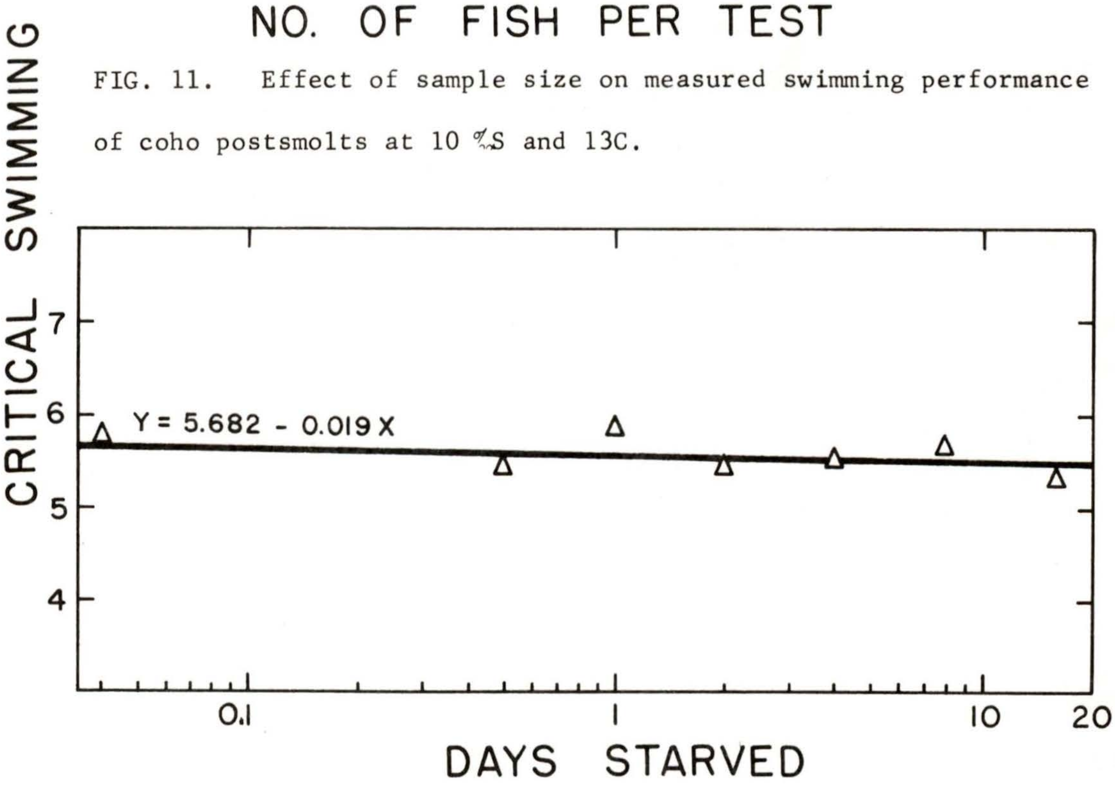

FIG. 12. Effect of starvation on swimming performance of coho fry in freshwater at 13C.

TABLE III Effects of sample size on critical swimming speed (L/sec) of coho postsmolts at 10 ‰S and 13C. Tests with more than one fish represent median values.

	1 fish	5 fish	10 fish
	5.20	4.55	4.85
	4.60	4.85	4.68
	4.17	3.65*	3.95*
	4.70		
	5.24		
Mean	4.78	4.35	4.49
$t_{.05(6)}$ =	2.447	t_s = 1.04 ns	t_s = 0.69 ns

* sample contained very aggressive dominant fish.

cribed by Hartman (1965) was observed within the experimental section of the test apparatus. During the early phase of a test, lateral and frontal displays predominated in establishing dominance hierarchy. As water velocities were progessively increased, threat nips, nips and chasing were observed. Dominant fish preferred to remain well upstream from the electric barrier and invariably displaced subordinate fish towards the rear of the experimental section. In such circumstances, subordinate fish were undoubtedly exposed to greater stress due to crowding at the downstream end of the test section and the increased possibility of fish in that area entering the electric field.

Figure 11 illustrates that reducing the sample size from 10 to 5 fish per test does not improve swimming performance significantly. Accordingly, because of substantial individual variability in stamina, it appears that ten fish per test provide the best measure of swimming performance when the experimenter is faced with time limitations. Nevertheless, the data suggest mean performance of juvenile coho measured in samples of 10 individuals, may be approximately 6% less than performance levels of which the animal is capable when tested singly.

B. Effects of starvation on performance

Agonistic behaviour among fish in the acclimation tanks was noted to influence frequency of feeding and amount of food consumed. This behavioural phenomenon was suspected of contributing to variation in swimming performance of the test fish.

Performance tests were conducted to determine whether moderate starvation would influence swimming ability. Employing routine procedures, these tests (September 11 - 27, 1971) used coho fry acclimated to and tested in fresh water at 13C. Prior to the experiments, each test group was held for one week under acclimation conditions and fed twice daily a diet identical to the outdoor stock. At the end of this period, food was withdrawn and groups were tested in the stamina tunnel at increasing intervals of starvation (Table IV). No significant difference was found in performance with starvation extended to 16 days (Fig. 12).

The data suggest that if subordinate fish were subjected to reduced food intake during entire acclimation period, this would not contribute appreciably to variation in swimming performance (Table IV). In addition, agonistic behaviour in the stamina tunnel did not appear to increase with starvation. Symons (1968) reported an increase in aggression and in strength of the social hierarchy among juvenile Atlantic salmon deprived of food for 3 days. The results also indicated that deprivation of food for a minimum of twelve hours prior to testing was not reducing performance capability.

Data Analysis

The data were analyzed by regression methods, using a second order non-linear polynomial as an empirical model (Lindsey and Sandnes, MS 1970). Response surfaces were constructed for each test series, yielding isopleths of performance in relation to test salinities and temperatures. The equation for the non-linear model is

$$Y^{\gamma} = b_0x_0 + b_1x_1^{\alpha_1} + b_2x_2^{\alpha_2} + b_{11}x_1^{2\alpha_1} + b_{22}x_2^{2\alpha_2} + b_{12}x_1^{\alpha_1}x_2^{\alpha_2}$$

where Y = critical swimming speed (L/sec); x_1, x_2 represent salinity (‰) and temperature (C), respectively; α_1, α_2 and γ are power

TABLE IV Critical swimming speeds of coho fry tested in freshwater at 13C at increasing intervals of starvation.

Days starved prior to testing	critical swimming speed (L/sec)
1/24	5.80
1/2	5.84
1	5.90
2	5.46
4	5.58
8	5.64
16	5.34

Mean

± 1 SD = 5.70 ± 0.17

Mean fork length of fish ± 1 SD = 5.13 ± 0.25 cm parameters estimated by maximum likelihood procedures (Lindsey et al, 1970).

In the case of the smolts (Group IV), the linear equivalent to the model was used ($\alpha_1 = \alpha_2 = \gamma = 1$). Analysis indicated that no improvement in the fit of the surface to the data would be achieved using the non-linear equation. Analysis of variance was conducted on the data in each test series (see Tables V - VIII).

The actual points for plotting response surface isopleths were obtained by transforming the polynomial to its canonical form (Box, 1956; Lindsey and Sandnes, MS 1970), reducing the equation to:

$$Y' - Y'_s = \lambda_{11} Z_1^2 + \lambda_{22} Z_2^2$$

where Y' = critical swimming speed in terms of Y^γ ; Y'_s = critical swimming speed at centre of surface; λ_{11}, λ_{22} = eigenvalues representing rate of change of response on the X_1-, X_2- surface; and Z_1, Z_2 = canonical variables, linear combinations of the x^α parameters.

Considerable difficulty was experienced in computing the power parameters for the advanced fry (Group II) data. It was impossible to differentiate between real and local maxima for α_1 (see Fig. 13). Values for the power parameters for this series were finally selected on the basis of minimum variance procedures.

The response surfaces generated by these analyses are a function both of the swimming speed data, and of the constraints of the second order polynomial used as a model to describe the regression relations. In general, a second order polynomial will describe an elliptical surface, with a "true" center, when response is maximized within the factor space investigated. When a response maximum occurs near or outside the boundaries of a factor space, surfaces other than the elliptical type may be generated. For example, if a maximum occurs within the factor space with respect to one test variable (e.g. temperature), but near or beyond the boundary of the factor space with respect to the second variable (e.g. salinity), the surface generated will often be a minimax. A minimax is a "saddle-shaped" surface in which response increases on one surface axis towards a local or provisional maximum in the center of the saddle, and also increases on the second surface axis toward the boundaries of the saddle (see Figs. 15-18). A minimax does not provide final information on the location of the true center of a response surface; it does provide information on the probable approximate location of the center. If circumstances permit iterative testing, the addition of further tests near or beyond the upper or lower limits of the second variable (e.g. salinity) would probably find a true center to an elliptical surface (Alderdice, 1972).

Estimation of Error

Assuming variance remained uniform over the field of test conditions, an estimate of average variability (± 2 S.D.) for the performance isopleths was found to be about ± 3% of calculated swimming speeds for fry (Group I, Fig. 15), and about ± 10% for smolts (Group IV, Fig.18). These calculations were based on data from the repeated tests of Tables IV (first eight days) and III (10 fish), respectively. The data necessary for computing such estimates were not available for the advanced fry (Group II) and presmolt (Group III) stages, but it is suspected they would lie somewhere in between the above values. Using the same calculation procedures, Griffiths (MS 1969) reported a variation of ± 7% for fish of equivalent size (9.5 cm) to the presmolt stage.

It is suspected that prolonged culturing, space limitations in the test apparatus and increasing aggressiveness with maturation, may have been important factors tending to increase variability in stamina of the older test fish.

RESULTS

Performance Surfaces

The maximum likelihood ratios (MLR) of the power parameters (α_1, α_2 and γ) used in the non-linear polynomial equations to construct the performance surfaces are shown in Fig. 13. The power parameters for the coho smolts (Group IV) are included for comparative purposes, although the results of the linear model were employed in constructing the response surface. With the exception of α_1 in the Group II series, plausible (MLR values $\geqslant 0.10$) values of the power parameters for all test stages are distributed over a narrow numerical range. Similarly, maximum likelihood ratios for levels of salinity (x_1) and temperature (x_2) estimated at the center (provisional or true) of the performance surface for Groups I-IV are indicated in Fig. 14. The range of plausible (MLR values $\geqslant 0.10$) temperature (x_2) values is relatively small compared to salinity (x_1). For the coho fry (Group I) and pre-smolts (Group III), plausible salinity values extended over most of the range of test salinities (0-20 ‰).

The analyses of variance (see Tables V-VIII) serve primarily as a statistical assessment of the relative importance of the linear, quadratic and interaction regression terms for salinity (x_1) and temperature (x_2) in the polynomial equation. For convenience, each of these tables follow their respective performance surface. The actual polynomial and canonical model equations used in the ensuing calcul-

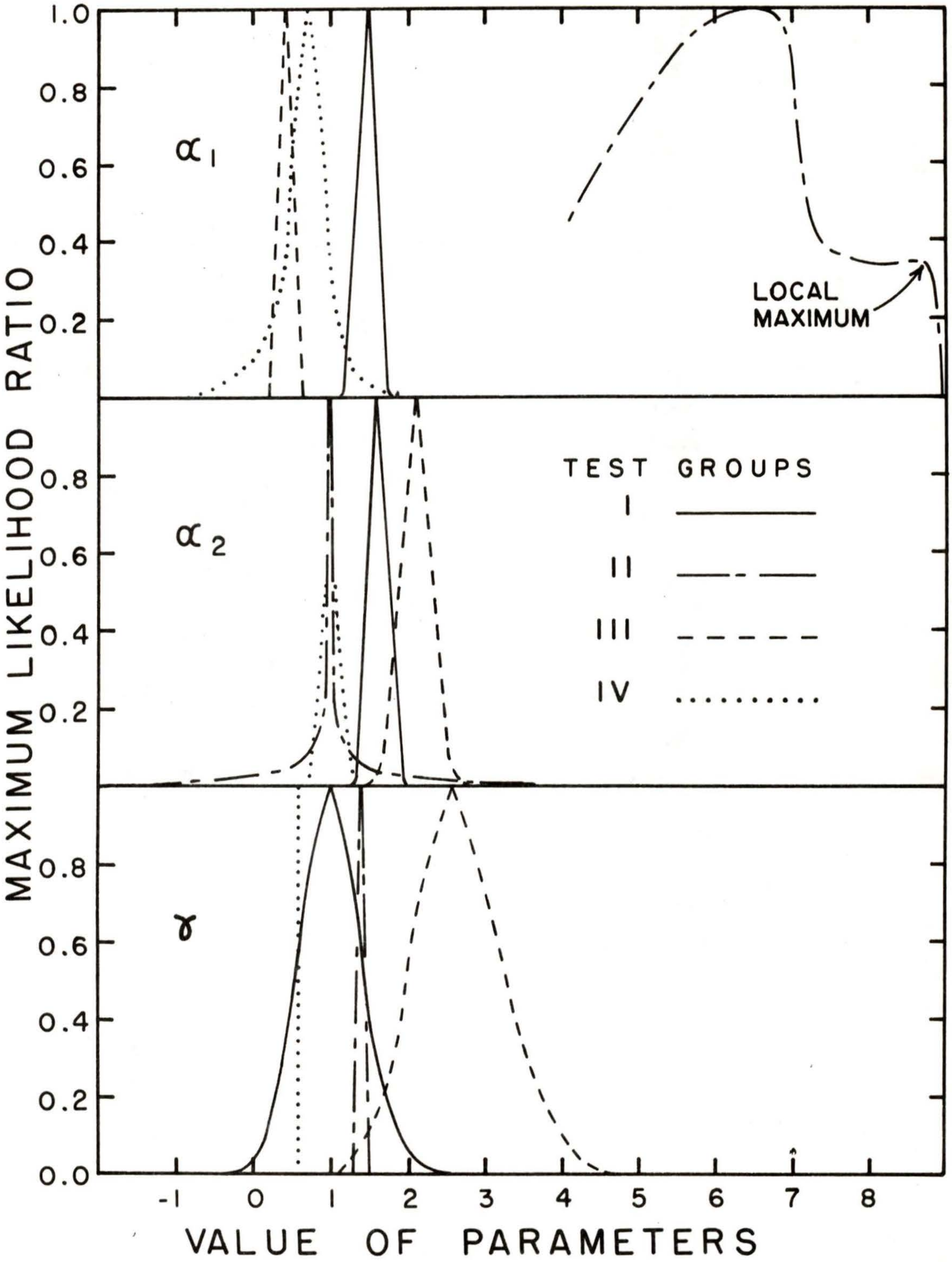

FIG. 13. Maximum likelihood graphs for various estimates of the power parameters of the nonlinear polynomial equations used to describe the relation between swimming speed, salinity and temperature in test Groups I-IV.

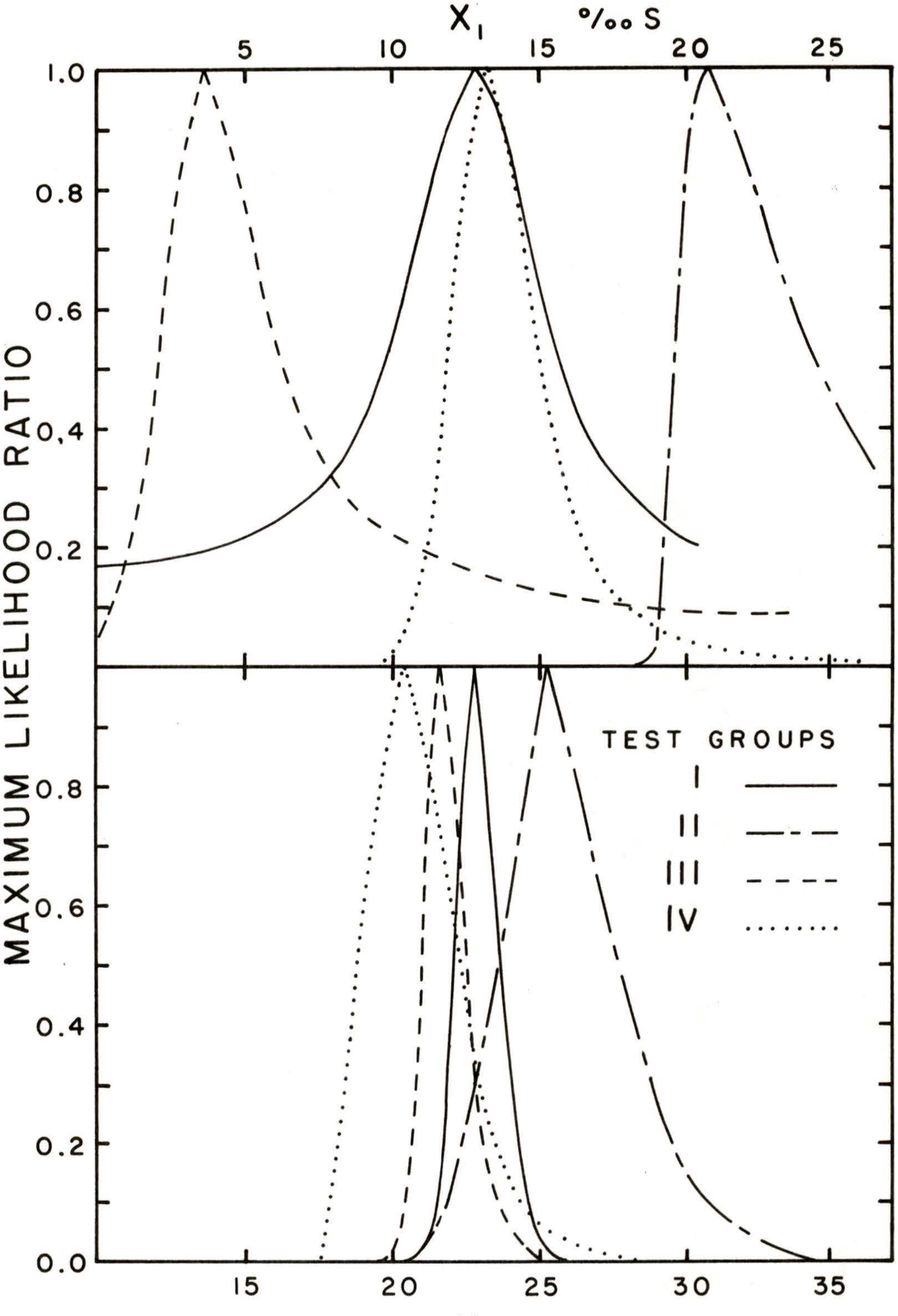

FIG. 14. Maximum likelihood graphs for levels of salinity and temperature estimated at the centre (provisional or true) of the performance surface for test Groups I-IV.

ations of the performance surfaces are included, indicating their respective numerical coefficients and power parameters. Maximum likelihood ratio (MLR) values in the analyses of variance clearly indicate the minor importance (MLR values $\gg 0.10$) of the salinity terms in the polynomial equation, compared to those of temperature. Despite the minor relative importance of salinity and salinity-temperature interactions, all terms were retained in the calculations since they represent the best estimates of salinity-temperature effects available from the data.

The performance surfaces (Figs. 15-18) illustrate isopleths of critical swimming speeds of the four seasonal stages of juvenile coho salmon tested. These are relative performance levels (fish lengths per second) expressed as a function of the salinity and temperature combinations of the factorial design. A close approximation of absolute velocities (cm/sec) can be obtained by multiplying relative performance by mean body length (Appendix I, Table V) of the respective test group. The estimated critical swimming speeds for the actual test combinations are shown in Appendix I, Tables I-IV. For all performance surfaces, the isopleths were extended slightly beyond the test space (dotted lines) to convey a better appreciation of surface configuration. These extrapolations should not be mistaken as actual biological measurements. The same criterion of reasoning was used for increasing the frequency of the response isopleths towards the center of the surface.

The performance surfaces reveal the following features. Maximum levels of performance in all stages (fry to smolts) occurred at temperatures near 20C. Relative swimming capacity of juvenile coho is approximately a linear function of temperature from 3C to those

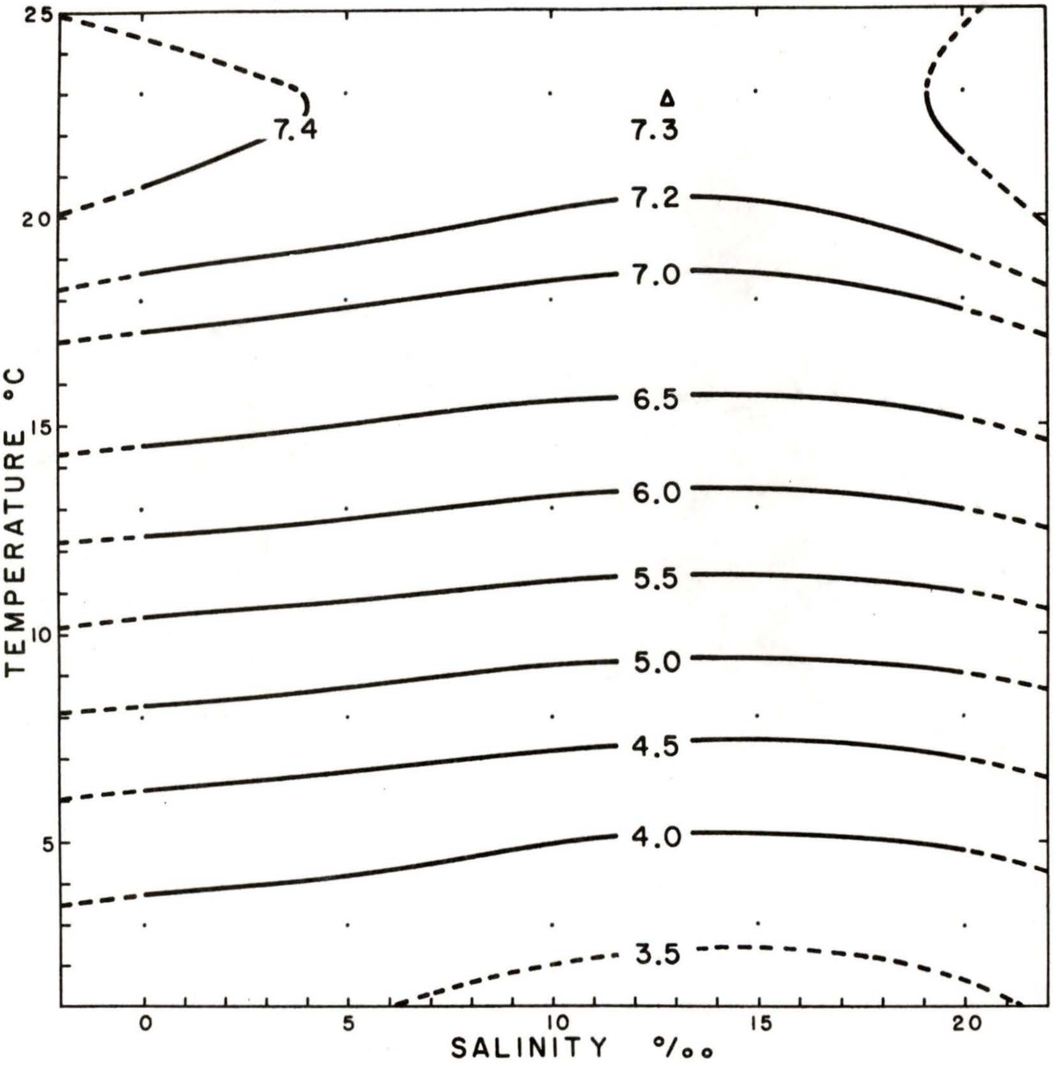

FIG. 15. Critical swimming speed isopleths (L/sec) for coho fry Group I) acclimated to salinity and temperature combinations (dots). Isopleths are shown by dashed lines outside the test space. Δ, in the figure is provisional maximum (see text).

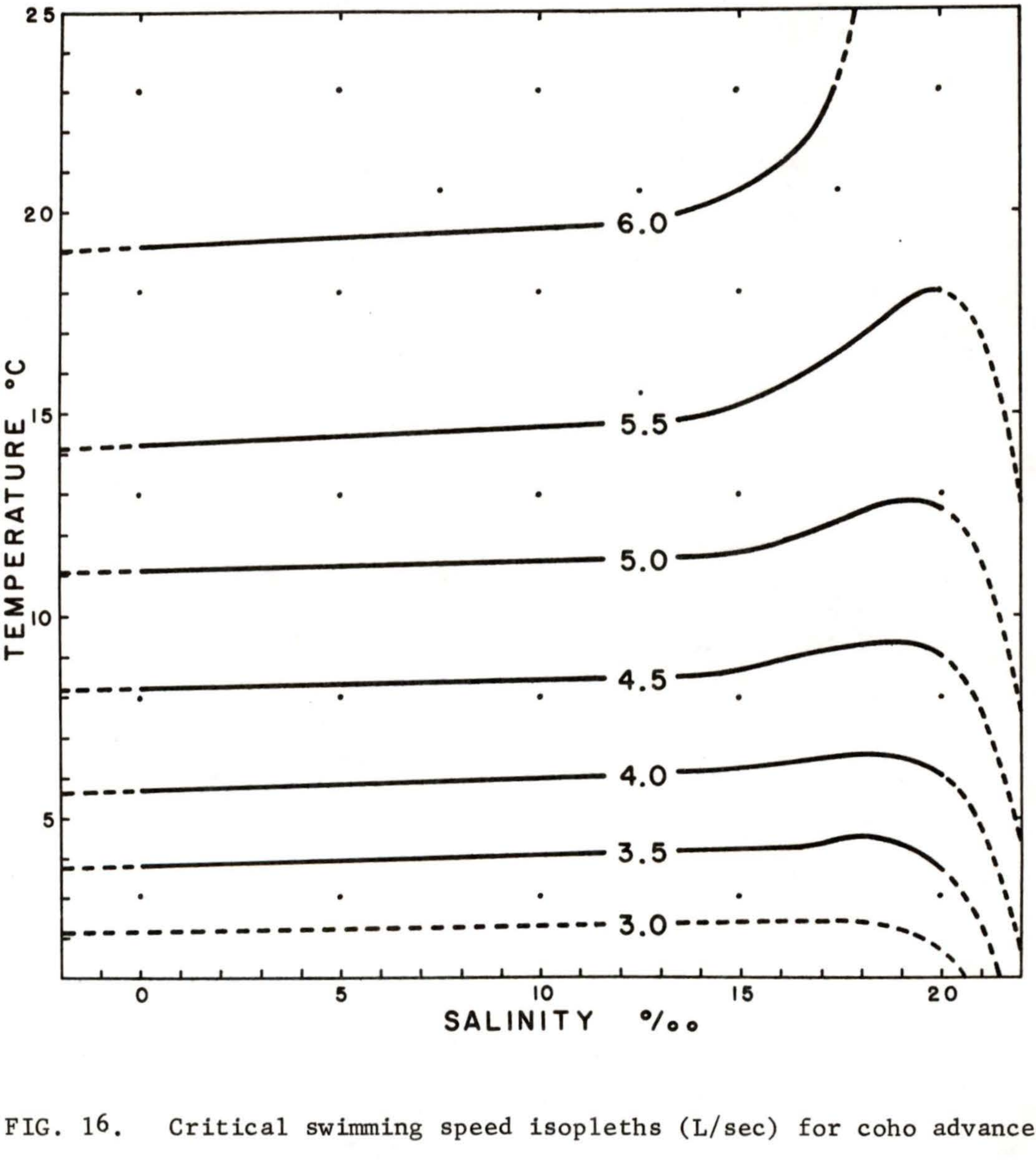

FIG. 16. Critical swimming speed isopleths (L/sec) for coho advanced fry (Group II). For explanation see Fig. 13. The provisional maximum was calculated to occur outside the test space at 20.68 ‰S and 25.18C.

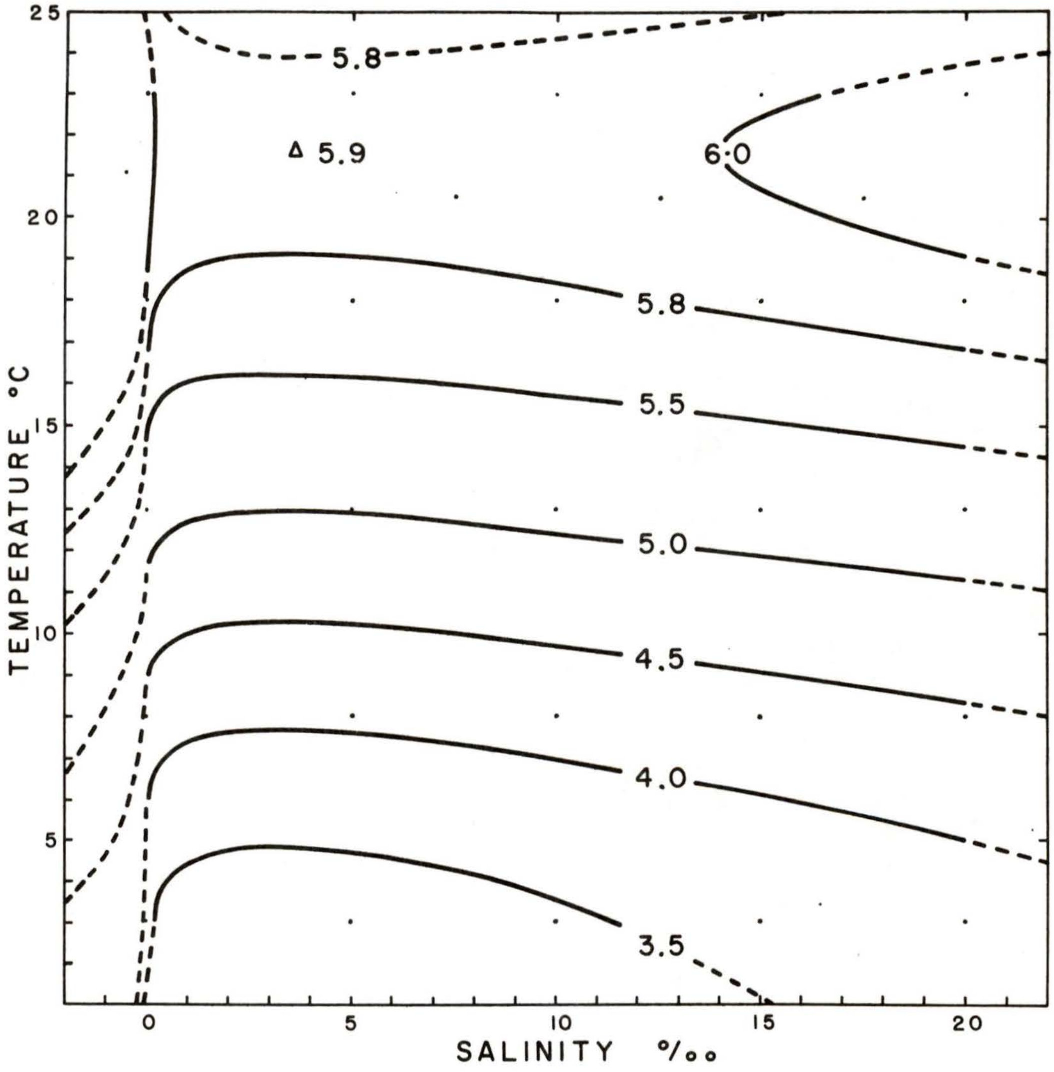

FIG. 17. Critical swimming speed isopleths (L/sec) for coho presmolts (Group III). For explanation see Fig. 13.

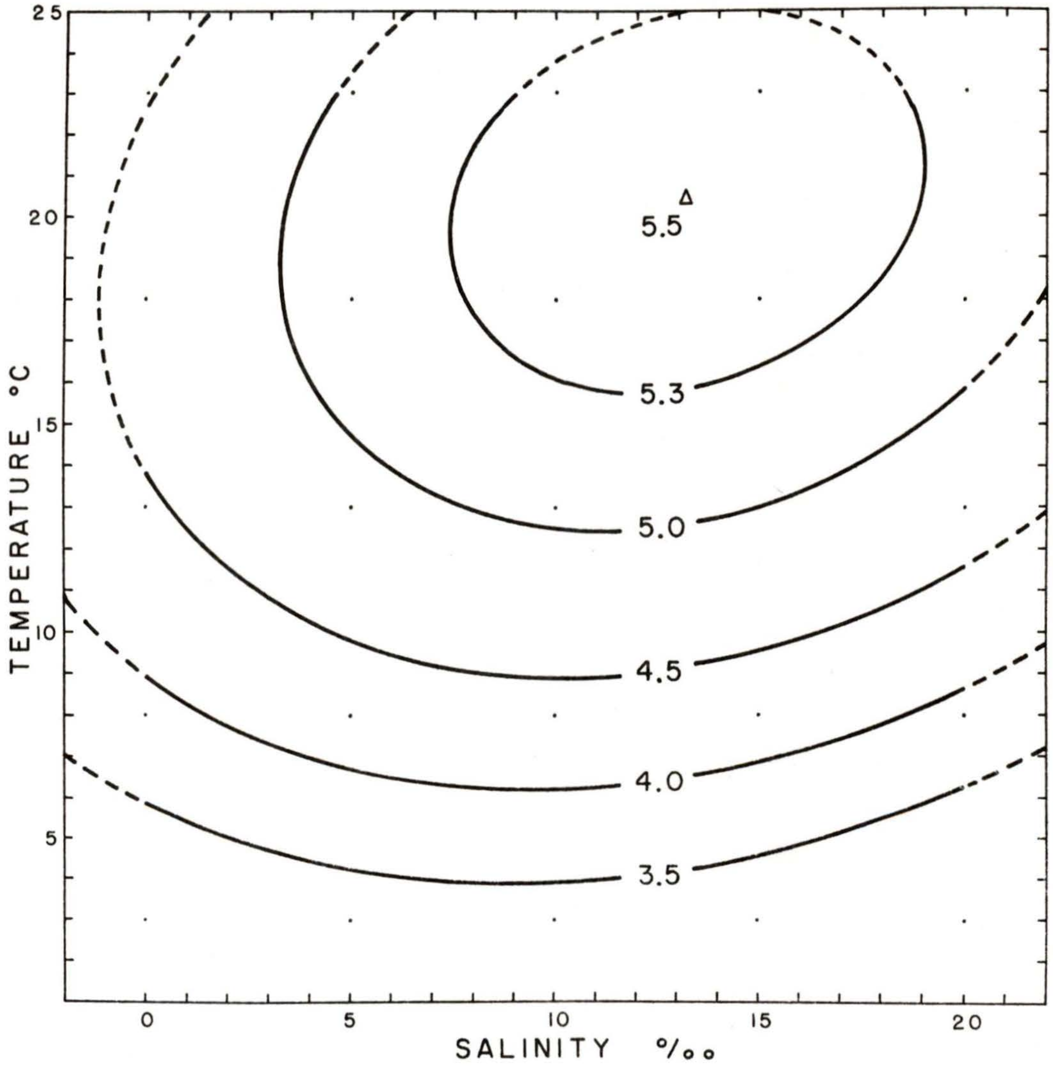

FIG. 18. Critical swimming speed isopleths (L/sec) for coho smolts (Group IV). The surface is an ellipse with Δ a final maximum.

temperatures associated with near-maximum performance. The nature of this relationship is indicated by the approximately equidistant separation of performance isopleths up to at least 15C.

The effect of salinity on swimming speed is much less pronounced. No unique or "true" response maximum was found for the fry, advanced fry or presmolts (Figs. 15-17). Isopleths of swimming speed tend to be flat over much of the range of salinities examined. Variance "explained" by the linear (x_1) and quadratic (x_1^2) terms associated with salinity is shown for each of the 4 test groups in the following table, a summary of terms from Tables V - VIII. The entries indicate whether or not a significant portion of the variance may be explained by an approximate F-test.

Group	I	II	III	IV
Terms: x_1	NS	S	NS	NS
x_1^2	NS	NS	S	S

The comparison suggests that salinity has no recognizable effect on the swimming performance of fry (Group I). An appreciable portion of the variance is associated with salinity in the advanced fry (Group II), but only in the linear term. In the remaining Groups (III, IV) there is also an appreciable portion of variance associated with salinity effects, but in the terms related to curvature of isopleths.

Examination of Appendix I, Table I, over the range of salinities tested at 18 and 23C, suggests that most estimates of critical swimming

TABLE V Analysis of variance of coho fry series using non-linear model. The two replicate series were pooled in the analysis.

Source of Variation	SS	df	MS	Approx F	MLR*
Regression	94.91	5	18.98	240.56	$0.89\text{x}10^{-37}$
Linear	86.95	2	43.47	550.96	$0.74\text{x}10^{-37}$
X_1	0.11	1	0.11	1.42	0.43
X_2	86.84	1	86.93	1100.50	$0.76\text{x}10^{-36}$
Quadratic	7.93	2	3.96	50.25	$0.36\text{x}10^{-13}$
X_1^2	0.27	1	0.27	3.43	0.13
X_2^2	7.66	1	7.65	97.06	$0.66\text{x}10^{-13}$
$X_1 * X_2$	0.03	1	0.03	0.41	0.78
Transform	0.66	3	0.22	2.78	$0.96\text{x}10^{-2}$
Residual	3.23	41	0.07		
Total	98.15	49			

*Components with MLR values greater than 0.10 could be deleted without significantly affecting the adequacy of the model (Lindsey et al, 1970).

Non-linear polynomial:

$$Y^{1.00} = 3.593 - 0.011x_1^{1.47} + 0.053x_2^{1.60} + 0.103\text{x}10^{-3}x_1^{2.95}$$

$$- 0.180\text{x}10^{-3}x_2^{3.20} + 0.162\text{x}10^{-4}x_1^{1.47}x_2^{1.60}$$

Canonical equation:

$$Y' - 7.301 = -0.180\text{x}10^{-3}\ Z_1^2 + 0.104\text{x}10^{-3}\ Z_2^2$$

The performance surface is saddle-shaped (mini max), indicated by opposing signs on the right hand side of the equation.

TABLE VI Analysis of variance of coho advanced fry series using non-linear model.

Source of Variation	ss	df	MS	Approx F	MLR
Regression	30.07	5	6.01	248.92	$0.77\text{x}10^{-26}$
Linear	28.85	2	14.42	597.11	$0.13\text{x}10^{-25}$
X_1	0.37	1	0.36	15.23	$0.27\text{x}10^{-3}$
X_2	28.30	1	28.30	1171.55	$0.18\text{x}10^{-25}$
Quadratic	0.90	2	0.45	18.70	$0.23\text{x}10^{-6}$
X_1^2	0.02	1	0.02	0.93	0.51
X_2^2	0.88	1	0.87	36.32	$0.30\text{x}10^{-6}$
$X_{1*}X_2$	0.24	1	0.23	9.87	$0.30\text{x}10^{-2}$
Transform	0.16	3	0.05	0.00	$0.16\text{x}10^{-1}$
Residual	0.48	20	0.02		
Total	30.55	28			

Non-linear polynomial:

$$Y^{1.38} = 3.160 - 0.139\text{x}10^{-8}x_1^{6.70} + 0.677x_2^{1.00} + 0.418x_1^{13.40}$$

$$- 0.112x_2^{2.00} - 0.167\text{x}10^{-9}x_1^{6.70}\ x_2^{1.00}$$

Canonical equation:

$$Y' - 5.747 = 0.480\text{x}10^{-17}Z_1^2 - 0.112\text{x}10^{-1}Z_2^2$$

Performance surface is saddle-shaped.

TABLE VII Analysis of variance of coho presmolt series using non-linear model.

Source of Variation	ss	df	MS	Approx F	MLR
Regression	22.96	5	4.59	69.64	0.45×10^{-18}
Linear	20.19	2	10.09	153.08	0.26×10^{-17}
X_1	0.01	1	0.01	0.20	0.86
X_2	20.18	1	20.17	305.99	0.27×10^{-17}
Quadratic	2.87	2	1.43	21.79	0.52×10^{-7}
X_1^2	0.31	1	0.31	4.75	0.45×10^{-1}
X_2^2	2.60	1	2.60	39.47	0.14×10^{-6}
$X_{1*}X_2$	0.00	1	0.00	0.04	0.96
Transform	0.99	3	0.32	0.00	0.30×10^{-3}
Residual	1.32	20	0.06		
Total	24.28	28			

Non-linear polynomial:

$$Y^{2.62} = 29.510 - 13.626x_1^{0.37} + 0.289x_2^{2.08} + 4.552x_1^{0.74}$$

$$- 0.238\times10^{-3}x_2^{4.16} - 0.153\times10^{-2}x_1^{0.37}x_2^{2.08}$$

Canonical equation:

$$Y' - 5.893 = 4.552\ Z_1^2 - 0.238\times10^{-3}\ Z_2^2$$

Performance surface is saddle-shaped.

TABLE VIII Analysis of variance of coho smolt series using linear model.

Source of Variation	ss	df	MS	Approx F	MLR
Regression	17.27	5	3.45	51.80	$0.27\text{x}10^{-4}$
Linear	13.45	2	6.72	100.81	$0.49\text{x}10^{-13}$
X_1	0.20	1	0.19	2.95	0.16
X_2	13.25	1	13.25	198.67	$0.58\text{x}10^{-13}$
Quadratic	3.46	2	1.73	25.95	$0.71\text{x}10^{-7}$
X_1^2	1.02	1	1.01	15.25	$0.63\text{x}10^{-3}$
X_2^2	2.44	1	2.44	36.64	$0.15\text{x}10^{-5}$
$X_{1*}X_2$	0.37	1	0.36	5.50	$0.42\text{x}10^{-1}$
Residual	1.27	19	0.06		
Total	18.54	24			

Linear polynomial:

$$Y = 2.160 + 0.077x + 0.273x - 0.482\text{x}10^{-2}x_1^2 - 0.747\text{x}10^{-2}x_2^2$$

$$+ 0.242\text{x}10^{-2}x_1x_2$$

Canonical equation:

$$Y' - 5.455 = -0.794\text{x}10^{-2}Z_1^2 - 0.435\text{x}10^{-2}Z_2^2$$

Performance surface is elliptical, with maximum performance at center of surface.

speeds at those temperatures, vary only within the range of experimental error. However, examination of all the data tends to show small but recurrent trends in swimming performance with respect to salinity.

Under the circumstances outlined, the following interpretation of salinity effects on performance is suggested. Changes in swimming performance with respect to salinity are small in all growth stages examined. Possible subtle differences associated with development are as follows. Swimming capacity at near-optimal temperatures appears to be minimal in coho fry at salinities of 13 - 15 ‰ or greater, in advanced fry at 18 - 20 ‰S or greater, in presmolts from about 0 - 15 ‰S, and in smolts in salinities above and below 20 and 10 ‰, respectively. The decline in swimming performance of advanced fry at higher salinities coincides with a decline in salinity tolerance noted for this stage (Alderdice, 1963 a; Conte et al, 1966; Otto, 1971).

The data (Appendix I, Tables I - IV) and surfaces suggest that maximum performance near 20C may occur in fry and advanced fry between 0 and 10 ‰S, in presmolts between 15 and 20 ‰S, and in smolts at or near a salinity of 15 ‰. Considerable further testing would be required in order to evaluate these interpretations.

Effect of Size on Swimming Performance

The data of all test Groups (I to IV) were pooled to consider the effect of size on swimming performance in relation to salinity and temperature. Brett (1965) has shown that the relation between body length and swimming speeds in sockeye salmon ranging from

7 - 50 cm in length, follows the general equation

$$Y = aX^b \text{ or } \log Y = \log a + b \log X,$$

where Y = swimming speed (cm/sec) and X = body length. In the present study, the restricted size range (4 - 12 cm) did not require transformation of the variables to achieve linearity. A simple linear regression, $Y = a - bX$, sufficed to express the relationship (Fig.19).

There is a substantial decline in the relative level of performance from a maximum near 7.2 lengths/sec in fry, to 5.5 lengths/sec in smolts. This is presumably a direct effect of increase in size and parallels similar findings by Bainbridge (1958) and Brett (1965). The results further indicate that the relation between size and relative swimming performance is temperature dependent, but independent of salinity. Temperature dependence is shown by the progressive change in slope of the relationship, and apparent extinction of this phenomenon at low temperatures (Table IX). With declining temperatures, smaller fish undergo a greater rate of decline in relative swimming performance. At 3C, all test stages attained swimming speeds of about 3.5 lengths/sec.

Comparison of Coho and Sockeye Performance

Critical swimming speeds of juvenile coho and sockeye salmon were compared at salinity-temperature test combinations along the diagonal of the factorial space (Fig. 9). The results indicated minor interspecific differences over the range of test conditions (Fig. 20).

Coho and sockeye advanced fry, acclimated to freshwater at 3.5C showed the following features: sockeye performed slightly

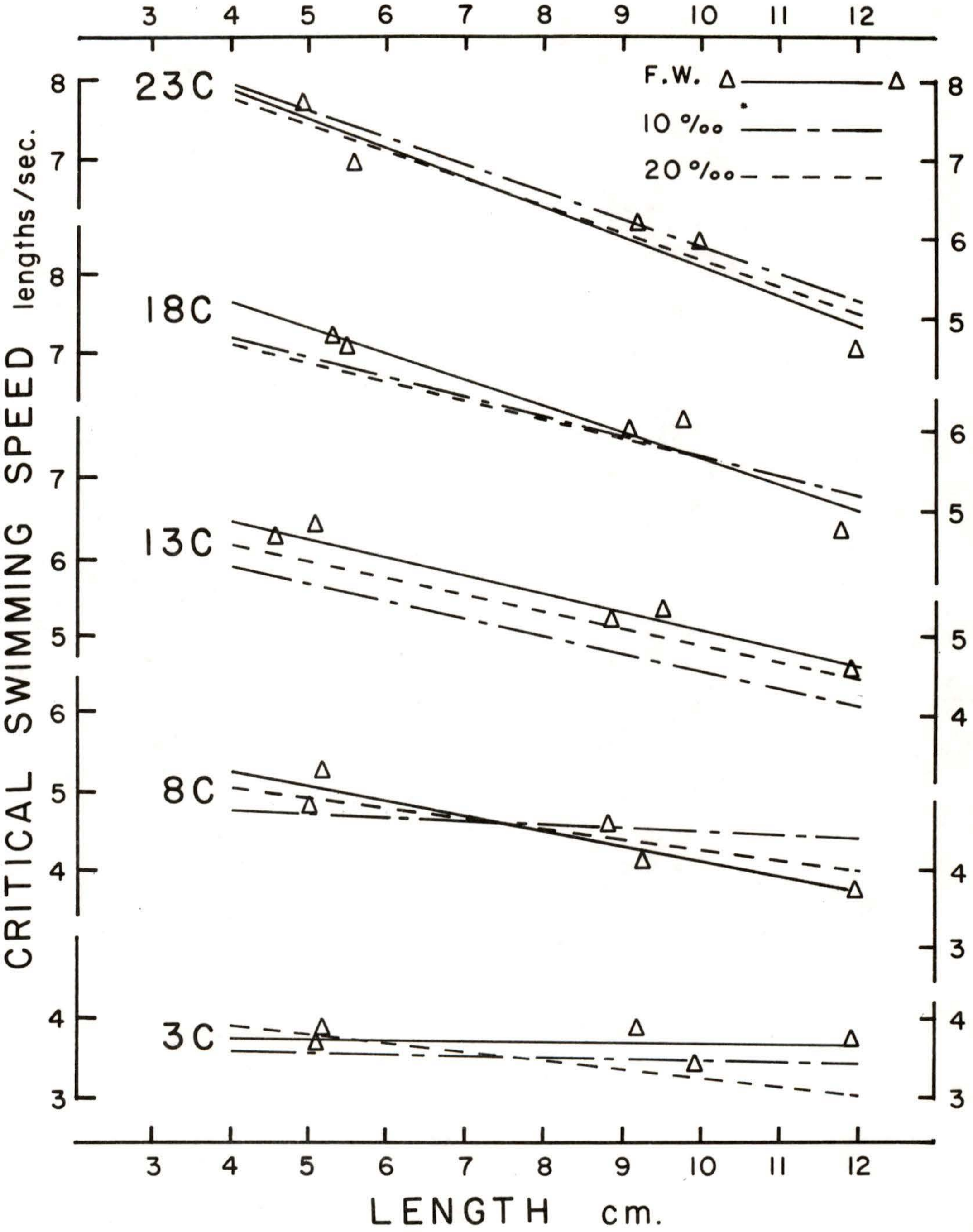

FIG. 19. Linear regression of critical swimming speed on fork length in juvenile coho salmon (fry to smolt stages). Relations are shown for fish acclimated to 3 levels of salinity (F. W., 10, 20 ‰) at each of 5 temperatures (3, 8, 13, 18, 23C). Median critical swimming speeds, on which the regression lines are based, are plotted for the freshwater (F.W.) tests.

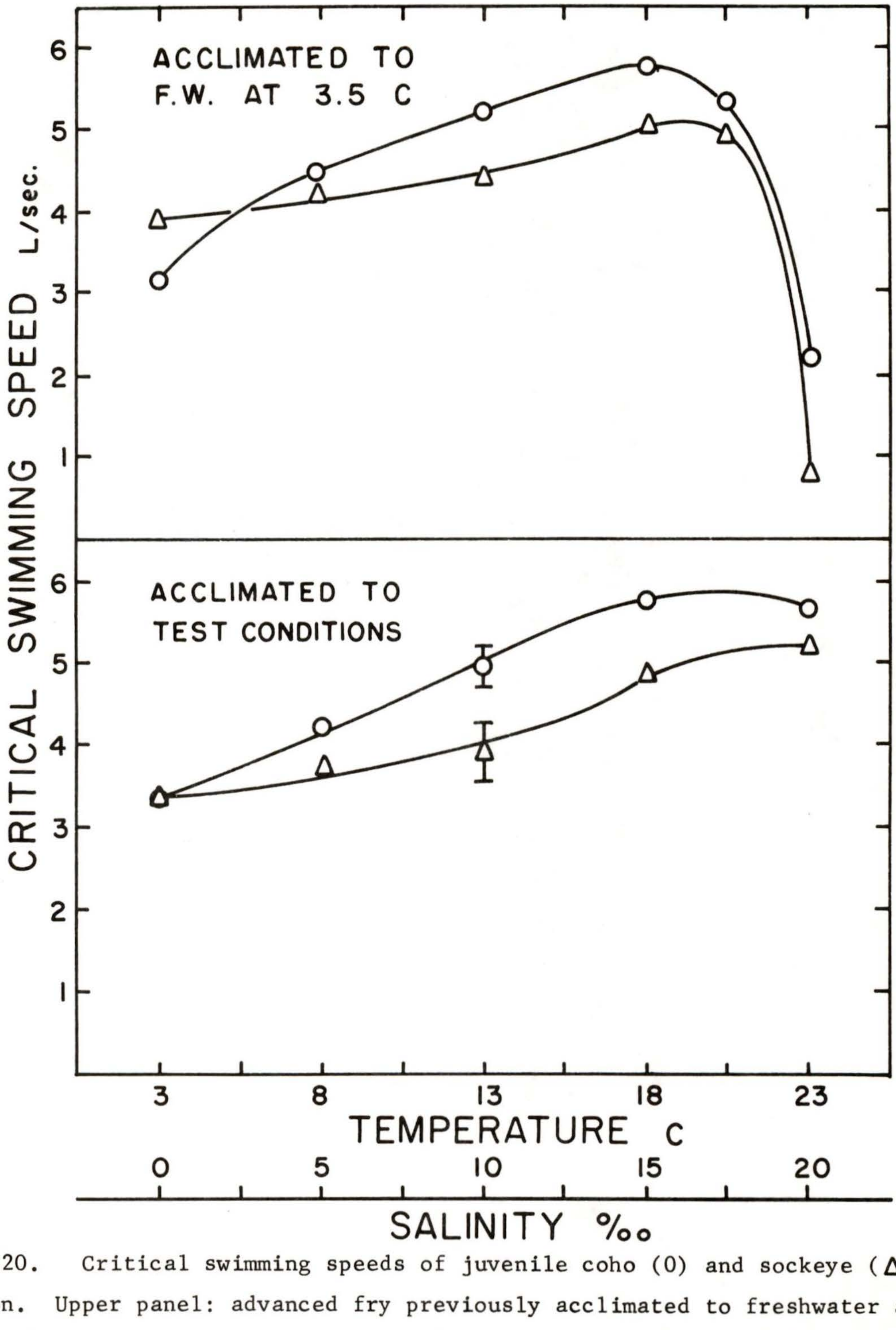

FIG. 20. Critical swimming speeds of juvenile coho (O) and sockeye (Δ) salmon. Upper panel: advanced fry previously acclimated to freshwater at 3.5C; lower panel: presmolts and smolts acclimated to test conditions. Test conditions in both cases are those on the diagonal of the factor space (see Fig. 9).

TABLE IX Regression equations for relation between critical swimming speed (Y, L/sec) and fork length (X, cm) for coho salmon (mean size, 4.52 - 11.95 cm) at various salinity-temperature combinations.

Salinity ‰	Temperature C	Equation
Freshwater	23	Y = 9.35 - 0.37 X
	18	Y = 8.95 - 0.33 X
	13	Y = 7.38 - 0.23 X
	8	Y = 5.99 - 0.19 X
	3	Y = 3.77 - 0.01 X
10	23	Y = 9.31 - 0.34 X
	18	Y = 8.19 - 0.25 X
	13	Y = 6.76 - 0.22 X
	8	Y = 4.93 - 0.04 X
	3	Y = 3.66 - 0.02 X
20	23	Y = 9.31 - 0.34 X
	18	Y = 8.08 - 0.24 X
	13	Y = 7.00 - 0.21 X
	8	Y = 5.59 - 0.13 X
	3	Y = 4.33 - 0.11 X

better than coho (by about one fish L/sec) in freshwater at 3C; for the salinity-temperature test combinations ranging from 5 - 20 ‰ and 8 - 23C, respectively, coho consistently attained higher levels of performance than sockeye (0.5 - 1.5 L/sec greater). At the extreme test combination of 20 ‰S and 23C, the swimming performance of both species declined markedly to a low 2.2 L/sec in coho and 0.8 L/sec in sockeye.

The combined performance of presmolt and smolt stages for coho and sockeye acclimated to test combinations along the diagonal of the factor space, reveals a swimming speed of 3.3 L/sec for both species in freshwater at 3C. At the extreme combination of 20 ‰S and 23C, near optimal levels of performance were attained for coho (5.6 L/sec) and sockeye (5.2 L/sec). Between test salinities of 5 - 15 ‰ and temperatures of 8 - 18 C, inclusive, interspecific differences in performance were similar to that obtained for fish acclimated to freshwater at 3.5 C (Fig. 20).

Differences Between Replicates

The two fully replicated test series conducted with the coho fry (Group I) provided an opportunity to compare variability between tests and to gain some appreciation of reliability of a single test series. Differences between replicates were tested using the 25 sets of observations of each series. No significant difference was obtained between replicates at $P < 0.05$ using a t-test ($ts = 0.50$). Similar maximum likelihood ratio (MLR) values in the analysis of variance (not included in text) for these two replicate series indicate that swimming performance over the field of test conditions was not appreciably different between replicate testing. In both replicates, linear (x_1) and quadratic (x_1^2) salinity terms, including the interaction term ($x_1 * x_2$), could be deleted (MLR $\geqslant 0.10$) from the polynomial equation without affecting the adequacy of the polynomial used as a model. Variability over the field of test conditions was least with coho fry in comparison with the other groups tested (see Appendix I, Tables I-V).

DISCUSSION

Comparison of Performance Surfaces

The effects of salinity and temperature in concert on swimming performance of juvenile Oncorhynchus kisutch revealed little change throughout premigratory stages of development. Concomitant with smoltification, swimming performance was differently affected by salinity and temperature, indicative of functional changes. In the interests of clarity, the performance surfaces of the various developmental stages will first be discussed separately from seasonal and size effects.

Combined effects of salinity and temperature indicated that swimming performance of juvenile coho was predominantly a temperature-dependent response during premigratory stages of development. Critical swimming speeds declined rapidly with decreasing temperatures from near maximum values (fry, 7.2 L/sec; advanced fry and presmolts, 6.0 L/sec) at about 20C to approximately 3.5 L/sec at 3C. Salinity effects on swimming capacity ranged from about 0.2 to 0.5 L/sec during the premigratory months of July - March. Brett (1965) stated that swimming speeds indicate the energy available to the fish after maintenance requirements (growth, metabolism, tissue repair, osmoregulation, etc.) have been met. The minor change in swimming performance with respect to salinity suggests maintenance costs were not appreciably different in freshwater from those in 20 ‰S. Coho advanced fry (Group II) revealed a decline of about 0.5 L/sec for tests beyond 15C and 15 ‰S, an environment containing relatively less dissolved oxygen compared to one of low salinity and temperature.

Swimming performance of coho fry (Group I) appears to operate independent of salinity. The almost flat configuration of the performance isopleths (Fig. 15) support this notion. The salinity effects obtained on later premigratory stages of development, although minor, are considered significant. For example, analysis of variance (Table VI, p. 42) indicated that linear (x_1) and interaction terms ($x_1 * x_2$) of the non-linear polynomial were of significant importance in the advanced fry (Group II) series. This was most likely a result of the greater salinity effects attained beyond 15 ‰S.

Coho smolts achieved maximum levels of swimming performance at salinities ranging from 8 - 18 ‰S (Fig. 18). Relative to this salinity optimum, swimming performance declined about 0.5 L/sec in freshwater and 20 ‰, suggesting maintenance costs were optimal at near isotonic salinities. Just prior to or concurrent with smoltification, coho appear to lose the somewhat euryhaline capacity to operate efficiently over the range of salinities noted in premigratory developmental stages, a phenomenon also noted for coho smolts by Alderdice (1963a) in terms of salinity tolerance.

The temperature effects and maximum sustained velocities obtained with coho advanced fry and presmolt stages are comparable to those reported by Griffiths and Alderdice (1972) for coho salmon (7.5 - 9.5cm) tested in the same apparatus. These authors investigated swimming speeds over a field of acclimation and acute (test) temperature combinations ranging from 2 - 26C in freshwater. Comparison with this work is therefore limited to trials conducted at equal acclimation and test temperatures (Fig. 21). Simple linear regression, Y = a + bX, expressed the relation between swimming speed and test temperature from 2 - 18C, yielding near identical slopes for both works. The regression lines indicate a low performance of about 3.2 L/sec at 2C and a near maximum of 5.6 L/sec at 18C. Both studies reveal that swimming performance of juvenile coho is linearly related to temperature up to at least 15C. An ultimate maximum performance was not clearly defined in the present study as the interval of 5C between tests was found to be excessive in the region of optimum temperatures. Griffiths and Alderdice show a maximum of about 6.0 L/sec at near 20C for tests conducted at intervals of 3C. It is conceivable that comparable levels of maximum performance would have been attained in the present study for similar test intervals. A more extensive experimental design was not considered in the current study so that effort could be directed toward an examination of seasonal changes in performance. Experimental time, therefore, was held at a minimum to reduce the possibility of occurrence of a progressive bias with changing size and physiological age of test animals. It has been documented that relative swimming performance declines with increasing size (Bainbridge, 1958, 1960; Brett, 1964, 1965).

Photoperiod and temperature have been suggested or shown to be important factors controlling seasonal physiological changes in fishes (Baggerman, 1960; Alderdice, 1963a; Beamish, 1964; Conte et al, 1965; Gross et al, 1965; Pinder and Eales, 1969; Saunders and Henderson, 1970). The fish in the present study were exposed to natural photo-

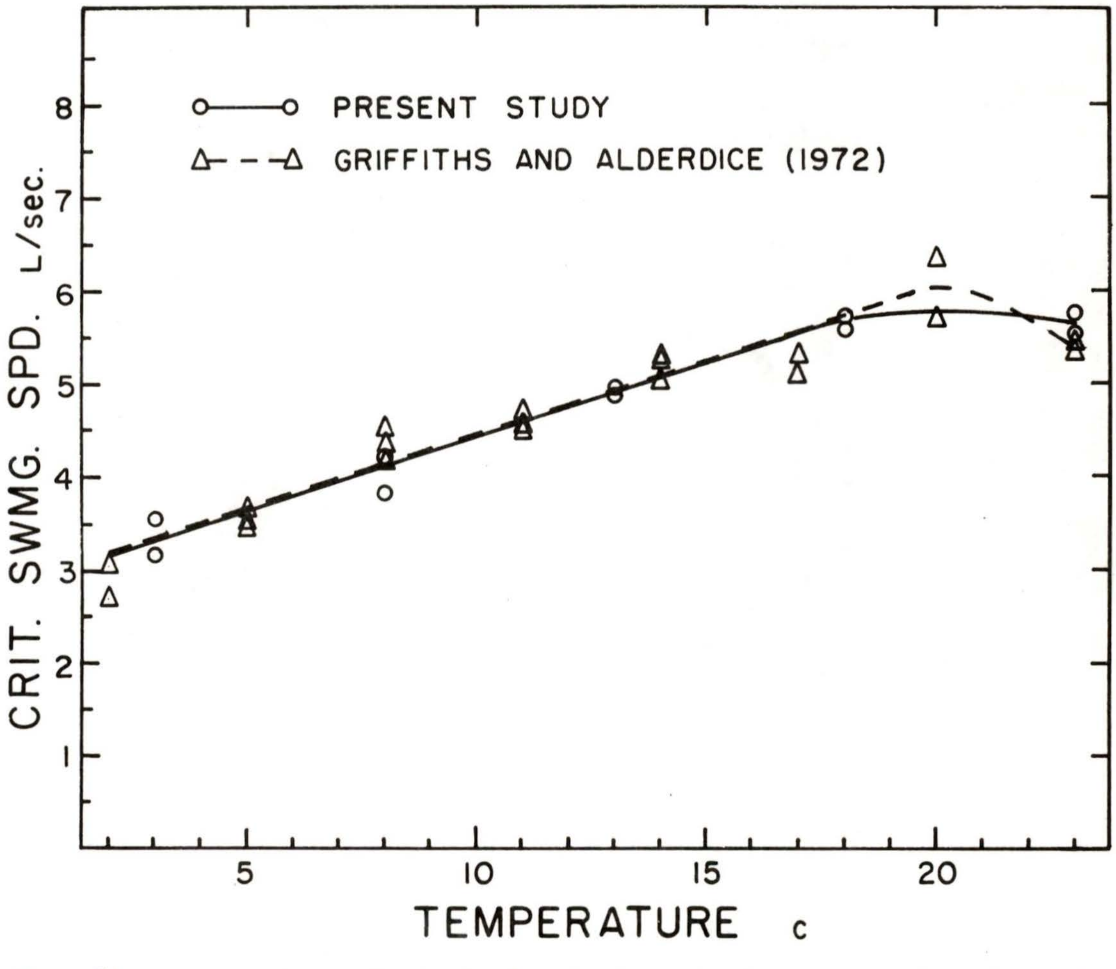

FIG. 21. Comparison of critical swimming speeds of juvenile coho salmon (advanced fry and presmolts) with those obtained by Griffiths and Alderdice (1972). Acclimation conditions are those at which the tests were conducted: freshwater, at the temperatures indicated. For the comparison, the current data (fork lengths/sec) have been adjusted to the scale (total lengths/sec) used by Griffiths and Alderdice (1972).

period and ambient freshwater temperatures. However, one can only assume their developmental response to salinity and temperature in relation to growth and smoltification was representative of wild population. Comparison of the response surfaces (Figs. 15 - 18) show no pronounced seasonal pattern of salinity and temperature effects on relative performance prior to smoltification, but subtle progressional changes are evident. It appears that near maximum adaptive capacity to salinity and temperature is attained in the early fry stage. Approximately 50% of optimum (ultimate maximum) swimming capacity (3.6 L/sec) in the fry, included temperatures down to 2C and salinities up to 20 ‰, with the relative effects of salinity and temperature estimated at 1:25 over the entire test space (Fig. 15). Clearly, swimming capacity of coho fry is not salinity-dependent to near lethal concentrations. Otto (1971) has shown that 22.5 ‰S at 10C is lethal to coho fry 4.43 cm long acclimated to freshwater. Somewhat similar results are reported by Conte et al (1966). It is difficult to understand how young coho are able to maintain optimum swimming capacity (7.2 L/sec) at salinities up to 2.5 ‰ below lethal concentrations. Presumably, acclimation is important in minimizing osmotic stress. Unfortunately, no experiments were conducted under acute salinity experience to test such assumptions.

With increasing size and physiological age, changes in relative swimming capacity were greater with respect to temperature than salinity. This can be illustrated numerically by comparison of the performance surfaces (Figs. 15 - 18). From 20 - 3C, relative swimming capacity declined by a factor of about 3.6 in fry (Group I) and 2.0 in smolts (Group IV), yielding a seasonal decline of temperature effects by a factor of 1.6. Similarly, from freshwater to 20 ‰, salinity effects on relative capacity ranged from a factor of 0.3 in fry to 1.0 in smolts, yielding an increased effect of 0.7 from fry-smolt stages. In smolts, the magnitude of temperature effects on relative capacity were about double that of salinity over the entire test space. It appears that juvenile coho have the adaptive capacity to minimize seasonal changes in performance over a range of salinities and temperatures. A change in relative capacity by a factor of about 0.7 - 1.6 from fry-smolts is considered a fairly stable response pattern.

Griffiths (MS 1969) observed no clear definition of seasonal changes in swimming performance between two test series of coho salmon (7.8 and 9.3 cm) examined during the months of September-April at a series of acclimation and test temperatures in freshwater. The prolonged period required to complete a test series and the lack of a distinct period between series were suggested as the most probable factors obscuring seasonal effects. The results of the present study indicated that seasonal changes were minimal in advanced fry and presmolt stages. This supports Griffiths' conclusions that refinement of experimental procedures are necessary to detect subtle differences. The difficulty encountered in the interpretation of swimming speed data is that changes in response to adaptive environmental variables (e.g. salinity) are slight, within the zone of tolerance, but may be more pronounced at near lethal levels. Fry (1967) has emphasized the relatively small differences obtained in swimming speeds compared with other temperature-dependent responses such as metabolic rate.

The seasonal changes in salinity preference reported for underyearling coho (Otto and McInerney, 1970) suggest that fish prefer the salinity zone which permits optimum locomotor capacity. Given a salinity gradient ranging from freshwater to 13 ‰, fish exhibited a bimodal preference from June to December for freshwater and 4.5 ‰S. In a gradient from 3 - 20 ‰S, preference was unimodal but progressively shifted from 7 ‰ in June to 13 ‰ in February. In the present study, coho smolts attained optimum locomotor capacity at about 13 ‰S. Definition of a salinity optimum in premigratory developmental stages was not clear.

Conte et al (1966) found no significant seasonal change in blood osmotic, sodium and chloride concentrations in coho fry-postsmolts held in freshwater, nor in their osmoregulatory capacity following exposure to 30 ‰ seawater. These authors concluded that seawater adaptation was well developed in fry and retained at this functional level into later developmental stages. Although juvenile coho remain homoiosmotic throughout the developmental stages, there is reason to speculate that maintenance cost of this physiological state is seasonally affected. In the present study, the attainment of optimum locomotor capacity at near isotonic salinities with smolts, may reflect a reduced energy cost in maintenance of the homoiosmotic state.

A final consideration of the performance surfaces is the effects of size and temperature on relative capacity. Comparison of fry and smolt stages (Figs. 15, 18) clearly indicate the influence of size. Bainbridge (1958, 1960) demonstrated that burst speeds of gold fish (Carassius auratus) and trout (Salmo irideus) declined with increasing size in accordance to the relation $Y = aX^b$, yielding slopes (b) of 0.71 and 0.58, respectively. Similarly, Brett (1964, 1965) reported a declining slope of 0.49 for sustained speeds of sockeye (7 - 53 cm long) determined at 15C. An examination of size effects in the present study revealed a similar decrease in relative capacity with increase in size but also a decline in slope (b) with decreasing temperatures (Table IX and Fig. 19). Smaller fish underwent a greater decrease in relative swimming capacity with declining temperatures, resulting in extinction of size effects at 3C; at this temperature all developmental stages performed at about 3.5 L/sec. Over the range of test temperatures relative swimming capacity of fry declined by a factor of 4.0 whereas smolts declined by a factor of 1.5. About 70% of the drop in relative performance occurred between 13 and 3C. Comparison of absolute performance from 23 - 3C revealed a decline from 38 - 18 cm/sec in fry and from 60 - 42 cm/sec in smolts. The decline in absolute capacity is about the same for both fry and smolts.

Differences in rate of decline in relative swimming capacity with temperature between fry and smolt stages may be due to differing rates of energy production, influenced by body musculature and metabolic scope. Fry appear incapable of operating efficiently at lower temperatures, thus the greater decline in relative swimming capacity.

Brett (1965) illustrated that the increased musculature and metabolic scope accompanying larger fish only partially compensated for increased hydrodynamic drag in sockeye, under the optimum temperature of 15C. The possibility that the relation between size and performance is temperature dependent has not been realized in the past. This aspect requires further investigation before pertinent comments can be made.

Osmoregulatory Capacity

Some evidence is available suggesting that the cost of osmoregulation is roughly proportional to the osmotic gradient between the medium and plasma of the fish. Rao (1968) showed that at various levels of activity, metabolic rate of rainbow trout (*Salmo gairdneri*) was minimal at the isotonic salinity of 7.5 ‰, attributable to reduced osmotic load. That is, in the isotonic medium less energy is used in osmoregulation, permitting greater scope for activity. Relative to this salinity optimum (7.5 ‰), the cost of osmoregulation was estimated to be about 20% higher in freshwater and in 15 ‰, but only 27% in a salinity of 30 ‰. These findings are in close agreement with the results reported for *Tilapia nilotica* (Farmer and Beamish, 1969) in a similar study.

The small salinity effects on swimming capacity of premigratory developmental stages are indicative of good osmoregulatory efficiency over a relatively broad salinity-temperature spectrum. Provided there is an opportunity to acclimate, underyearling coho have the physiological capacity to move from freshwater to brackish environments with no appreciable change in locomotor capacity. Smolts appear to lose their euryhaline capacity, showing a decline of 0.5 L/sec in freshwater and 20 ‰S, with optimum levels of performance at near isotonic salinities.

There is considerable evidence to support the notion that young coho are good osmoregulators. Black (1951) found no appreciable difference in osmoregulatory capacity of freshwater acclimated coho and chum salmon fry when transferred into salinities of about 16 ‰. Chum salmon go to sea as fry. In salinities ranging from 27 - 30 ‰, the coho fry, unlike the chum fry, lost more body water and were incapable of survival beyond 36 hours. Similar mortalities for young coho fry have been reported by Coche (1967), who further indicate that such salinities could be tolerated if the animal were acclimated below sublethal concentrations. More recently, Otto (MS 1968, 1971) has shown that the upper incipient lethal salinity (that salinity at which 50% of the animals tested were calculated to survive the effects of salinity indefinitely) for coho fry transferred directly from freshwater, extends from 22 - 25 ‰ during the months of May to October.

The stability of osmoregulatory capacity in juvenile coho with increasing size and physiological age was demonstrated by Conte et al (1966). These authors showed that early coho fry to postsmolt stages acclimated to freshwater retained a constant regulatory capacity up to two years of age. In all developmental stages tested, the osmotic, sodium and chloride blood concentrations were held at near freshwater levels for fish exposed to 30 ‰S. The osmoregulatory system appears to attain its full potential function in the fry by the month of July and is retained in this state into later juvenile stages of development. In contrast, steelhead trout (Conte and Wagner, 1965) and Atlantic salmon (Houston, 1960; Parry, 1960) showed a progressive development of adaptive capacity more closely related to the chronological period of seaward migration.

It is of particular interest that the fry (Group I) showed no evidence of declining swimming performance at high salinity-high temperature combinations, an environmental situation in which osmotic costs are presumably relatively high and dissolved oxygen appreciably less. Brett (1965) has shown for sockeye that the cost of supporting metabolism for swimming at a given absolute speed increased with decreasing size, in spite of reduced hydrodynamic drag. It is possible that the salinity acclimation process alters the availability and utilization of oxygen in a way which does not markedly influence energy requirements for osmoregulatory purposes.

Ample laboratory evidence has been provided indicating juvenile coho are good osmoregulators. However, the mechanisms and sites of osmoregulation in juvenile salmonids are not well documented. Potts (1954) suggested the energy expended in osmotic and ionic regulation is a function of the animal's permeability, surface area, and concentrations of the blood, urine and external medium. Production of urine hypotonic to the blood in a freshwater animal markedly reduces osmotic work and is compatible with high osmoregulatory efficiency. In brackish water this kind of mechanism has little effect in reducing osmotic work, suggesting that juvenile coho utilize other means to attain good osmoregulatory efficiency over a range of salinities and temperatures. Parry (1958) reported that the epithelium of young salmonids is well supplied with mucous secretory cells, which probably contribute to integumentary impermeability. Gordon (1963) indicated that the important process in salinity acclimation of rainbow trout was a reduction of integumentary permeability to water; hence osmotic costs may not differ appreciably over a range of salinities. Such potential adaptation mechanisms, coupled with the development of an efficient salt-regulatory ability across the respiratory epithelium of the gills, may operate in young coho salmon.

The large acidophilic epithelia cells in the gill filaments of salmon have been suggested to perform a chloride secretory function in a marine environment (Threadgold and Houston, 1964). In Atlantic salmon, these cells increased in density during the parr-smolt transformation and degenerated in the postsmolt stage, suggesting their importance may be related to the smoltification process and seaward migration. No evidence has yet been shown that greater cell density is associated with increased efficiency in osmoregulation nor that they do, in fact, salt-regulate.

There is the possibility that the relative unimportance of salinity on swimming capacity of juvenile coho does not necessarily reflect high osmoregulatory efficiency. The body tissues may tolerate short term deviations from the normal osmotic concentration level. Although Conte et al (1966) showed that inactive juvenile coho maintained homoistasis of the blood plasma when immersed in sea water (30 ‰), the outcome may be different in exercised fish. Rao (1969) reported that activity influenced the blood osmotic concentration of rainbow trout at 30 ‰S, yielding higher levels in exercised fish than in resting individuals. In the present study, the coho forced to swim at maximum sustained speeds probably developed a slight osmotic debt, regaining the homoiosmotic state during the post-fatigue period.

Ecological Considerations

The results of the present study show that sustained swimming performance of normally freshwater resident underyearling coho is little affected by salinities up to at least 20 ‰. They are capable of adaptation to a range of salinities and temperatures in the fry stage of development and retain this capacity into later juvenile stages. Typical of coho stream habitats are marked seasonal fluctuations in water temperatures and flow. Temperatures of freshwater nursery areas may vary from near freezing in winter to about 20C in summer when water depth and flow are usually minimal. Likewise, tidal influence may result in marked daily fluctuations of salinity structure at the mouth of the parent stream. No documented field evidence has indicated that underyearling coho inhabit estuarine areas. However, their ability to maintain reasonably high levels of swimming performance over a broad range of salinities and temperatures suggests that a critical re-examination of the conventional life history pattern would be desirable. Over the field of test salinities, swimming capacity was not depressed beyond 0.5 L/sec for any of the developmental stages tested. A decline of this magnitude is not considered an appreciable limitation on locomotor-dependent activities. It, therefore, seems reasonable to postulate that the large numbers of presmolt emigrants should be expected to survive early entry into the sea.

Otto (1971) conjectured that survival of presmolt emigrants might be possible if the estuary of the parent stream allowed an opportunity for the salinity acclimation process to occur. Presumably, the fish would prefer those salinities permitting optimum growth and osmoregulatory capacity (Otto and McInerney, 1970) thus improving their chances of survival in time through development of increased capacity to tolerate higher salinities (Otto, 1971). Acclimation should allow survival of presmolt emigrants at sea, which in turn, should be reflected in the fishery. The paradox is that about 97.5% of the coho fishery in the offshore waters of British Columbia are reported to be animals which entered the sea in their second year of life (Foerster, 1955). Likewise, reports on the contribution to the coho fishery by presmolt emigrants ranges from 0.1% (Pritchard, 1940) to 2.6% (Milne, 1962). The negligible numbers of presmolt emigrants taken in the fishery is difficult to appreciate, since laboratory works show that measures of sustained swimming performance and growth (Canagratnam, 1959; Otto, 1971) of underyearling coho in brackish salinities are comparable to those obtained under freshwater conditions.

It is possible that a high predator density at the mouth of the estuary is responsible for the drastic reduction in the presmolt emigrant contribution to the fishery. Parker (1968) has estimated that coho smolts holding in a saltwater inlet can markedly reduce the numbers of pink and chum salmon fry migrating seaward. Cannibalistic behaviour is common amongst juvenile salmonids and may well be an important factor reducing the survival of coho fry emigrants within the estuary. Since the timing of both the coho fry and smolt emigrations roughly coincide (P. Wickett, unpublished data), coho smolts may be a major predator of the young fry in the estuary. In the absence of territory and appropriate cover, young coho would be vulnerable to predation by larger salmonids because of their lesser absolute sustained swimming capacity.

The feasibility of rearing coho presmolt emigrants in saltwater impoundments as a means to increase production of the fishery has been emphasized by Coche (1967) and Otto (1971) based on evidence of salinity tolerance in the underyearling stage. Further evidence to support this notion has been provided by the current study. Swimming performance of underyearling coho is not depressed in salinities up to 20 ‰. The possibility of increasing the fishery by rearing presmolt emigrants in salt water impoundments has been demonstrated with hatchery-reared coho fry (Garrison, 1965). In this study, growth and smoltification which normally require a one year period of freshwater residency were attained within a period of three months in a saltwater rearing pond.

Evolutionary Significance

The results of the present study indicate that underyearling coho have the physiological capacity to move between freshwater and brackish environments without showing appreciable changes in swimming performance. The significance of this early adaptation to seawater is not clear in view of their conventional life history in which a year of stream residence precedes a well defined period of smoltification and seaward migration. One possibility is that this early "pre-adaptation" to seawater serves as a species dispersal mechanism to alleviate population pressure in the parent stream. Since swimming performance of underyearling coho is not depressed in brackish salinities, it is conceivable that colonization of nearby uninhabited freshwater areas, if available, could be achieved during the juvenile stage.

A consideration of the evolutionary history of the genus Oncorhynchus may offer other valid reasons for early seawater development in coho salmon. The ability of coho fry to cope with salinities up to at least 20 ‰ may reflect a retention of their probable marine origin (Shmidt, 1936, quoted by Chernenko, 1969). On the other hand, if one accepts the freshwater theory of ancestry, present day coho population may be evolving a reduced period of freshwater residency. Shmidt (1936) believed Oncorhynchus to be the primitive salmonid of the Pacific Ocean on the evidence of morphological features and on their mode of life. He suggested that Salmo was more likely a derivative of the genus Oncorhynchus or of a common ancestor. Tchernavin (1939) propounded that Oncorhynchus was of freshwater ancestry, an hypothesis which received acceptance by later authors (Milne, 1948; Hoar, 1958; Neave, 1958) but there was conflict as to whether Oncorhynchus originated from the Pacific Salmo or from a trout-like ancestor common to both. More recently, karyotype comparison has suggested that salmon of the genus Oncorhynchus originated from the Pacific _Salmo_ (Simon, 1963; Chernenko, 1970), with speciation proceeding in the order: chum → chinook → coho → sockeye → pink salmon. Chum and pink salmon by this scheme are rather distantly related and represent convergent adaptation in their seaward migration as young fry. This pattern is considerably different from that proposed by Milne (1948) and Hoar (1958) who regarded _O. kisutch_ as the most primitive species in the genus and traced speciation in the order: coho → chinook → sockeye → chum → pink salmon. Since the method used by Simon and Chernenko is based on the evolution of chromosome systems, their pattern of speciation may more closely represent the true evolutionary line. These findings suggest that the coho have changed from their Pacific _Salmo_ ancestor. In line with this view the present study may be interpreted as evidence for a reduced period of freshwater residency.

SUMMARY

1. The effects of salinity and temperature acting in concert on sustained swimming speed of 4 seasonal stages of juvenile coho (4.9 - 11.4 cm), acclimated to test conditions were examined in a stamina tunnel.
2. Fish were acclimated to test salinities and temperatures at the rate of 2.5 ‰S/day (± 0.5 ‰) and 1C/day (± 0.10C), respectively.
3. Samples of ten fish were used in performance tests; water velocity was increased every hour at increments of approximately one-eighth of maximum sustained velocities, until last fish fatigued. Critical swimming speeds were calculated as estimates of maximum sustained speeds.
4. The effects on swimming performance of test group size and starvation up to 16 days were non-significant. However, performance in samples of ten fish was approximately 6% less than for fish tested singly.
5. Response surface analysis employing a second order polynomial was used to construct the relation of critical swimming speed to test parameters of salinity and temperature.
6. Relative swimming capacity in all test stages was approximately a linear function of temperature from 3C up to at least 15C. Within this temperature range all test stages revealed an increase in absolute swimming performance of about 20 cm/sec.
7. Salinity effects were small in coho fry to presmolt developmental stages. Swimming capacity of fry appears to be in-

dependent of salinity levels below 20 ‰. Salinity effects on performance in advanced fry and presmolts were small but statistically significant. Swimming speeds of coho smolts was about 0.5 L/sec greater at near-isotonic salinities than in freshwater and in 20 ‰S. This suggests reduced osmotic cost at the salinity optimum.

8. All test stages attained greatest measured swimming capacity near 20C, ranging from 7.2 L/sec in fry (5.0 cm) to 5.5 L/sec in smolts (11.4 cm). This decline in relative swimming capacity was attributed to increased size. Size effects diminished with decreasing temperatures; relative performance was independent of size at 3C and 3.5 L/sec in all test stages.
9. The results suggest locomotor-dependent activities of underyearling coho are not depressed in salinities up to at least 20 ‰ and that underyearlings are physiologically equipped to survive early entry into the sea.

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APPENDIX I DATA FOR THE COHO DEVELOPMENTAL STAGES TESTED

TABLE I Coho fry, Group I, tested July 29 - August 25, 1971.

Random test order	Salinity ‰	Temperature C	Mean fork length cm	Critical Swg.spd. L/sec
1	5	3	4.42	4.30
2	10	13	4.49	5.60
3	0	23	4.89	7.70
4	0	13	4.53	6.25
5	20	18	4.73	7.08
6	20	8	4.63	5.05
7	15	8	4.53	3.98
8	10	3	4.78	3.35
9	15	23	4.97	7.42
10	20	13	5.04	5.96
11	5	8	4.83	4.95
12	0	18	5.27	7.20
13	10	8	4.97	5.02
14	5	18	5.07	7.40
15	5	23	5.39	7.40
16	10	23	5.29	7.96
17	15	3	5.05	3.56
18	15	18	5.05	7.01
19	15	13	5.04	6.32
20	20	23	5.17	7.48
21	5	13	5.02	6.10
22	0	8	5.11	5.24
23	10	18	5.16	7.20
24	0	3	5.08	3.68
25	20	3	5.18	3.75

APPENDIX I (cont'd)

TABLE Ia Coho fry, Group I (replicate series) tested August 26 - October 1, 1971.

Random test order	Salinity ‰	Temperature C	Mean fork length cm	Critical swg.spd. L/sec
1	0	13	5.02	6.40
2	0	3	5.15	3.82
3	10	23	5.28	7.16
4	20	3	4.93	3.68
5	5	18	5.18	6.82
6	15	8	4.98	4.60
7	20	23	5.34	7.38
8	0	23	5.54	6.98
9	10	3	5.11	3.82
10	20	13	5.08	5.98
11	10	13	4.97	6.04
12	5	8	4.96	4.80
13	15	18	5.20	7.04
14	5	13	4.95	5.60
15	15	13	5.05	5.64
16	20	18	5.14	6.75
17	20	8	4.96	4.84
18	5	23	5.48	7.24
19	0	8	4.97	4.80
20	5	3	4.94	3.54
21	10	8	5.07	4.54
22	10	18	5.29	6.60
23	0	18	5.45	7.08
24	15	3	4.89	3.66
25	15	23	5.45	7.26

APPENDIX I (cont'd)

TABLE II Coho advanced fry, Group II, tested November 16 - December 30, 1970.

Random test order	Salinity ‰	Temperature C	Mean fork length cm	Critical swg.spd. L/sec
1	5	8	8.95	4.27
2	15	18	10.10	5.84
3	10	13	8.63	5.52
4	10	8	9.32	4.53
5	0	3	9.89	3.40
6	20	3	9.12	3.20
7	15	3	8.09	3.15
8	15	13	9.20	4.80
9	10	18	8.94	5.90
10	5	3	8.11	3.05
11	5	18	9.49	5.90
12	0	8	8.77	4.55
13	0	23	9.13	6.20
14	20	23	9.04	5.60
15	15	8	9.11	4.40
16	20	18	9.35	5.59
17	5	23	8.80	6.40
18	20	8	8.48	4.50
19	5	13	8.63	5.40
20	10	23	8.43	6.36
21	10	3	8.27	3.37
22	15	23	8.65	6.28
23	20	13	8.65	5.03
24	0	13	8.81	5.20
25	0	18	9.02	6.00
26	12.5	15.5	8.71	5.60
27	17.5	20.5	8.98	5.98
28	7.5	20.5	8.87	6.08
29	12.5	20.5	8.98	6.09

APPENDIX I (cont'd)

TABLE III Coho presmolts, Group III, tested March 15 - April 19, 1971.

Random test order	Salinity ‰	Temperature C	Mean fork length cm	Critical swg. spd. L/sec
1	5	3	9.59	2.35
2	10	8	9.67	4.33
3	5	8	9.58	4.20
4	5	13	9.74	5.28
5	20	8	9.64	4.58
6	10	13	9.80	5.24
7	20	13	9.82	4.90
8	0	8	9.21	4.12
9	20	3	9.24	3.85
10	0	3	9.19	3.84
11	20	23	10.03	5.94
12	15	13	9.44	5.10
13	15	8	9.62	4.48
14	15	23	9.80	6.08
15	20	18	9.57	5.98
16	0	13	9.48	5.34
17	0	18	9.74	6.14
18	15	3	9.13	3.60
19	15	18	9.73	6.00
20	5	23	9.88	6.00
21	10	3	9.25	3.67
22	10	18	9.64	5.77
23	5	18	9.78	5.66
24	10	23	9.99	5.90
25	0	23	9.96	5.96
26	12.5	15.5	9.60	4.98
27	7.5	20.5	9.40	5.66
28	12.5	20.5	10.10	5.90
29	17.5	20.5	9.85	6.24

APPENDIX I (cont'd)

TABLE IV Coho smolts, Group IV, tested May 27 - June 23, 1971.

Random test order	Salinity ‰	Temperature C	Mean fork length cm	Critical swg.spd. L/sec
1	5	13	10.80	5.40
2	20	23	11.15	5.42
3	5	3	10.93	3.40
4	10	18	11.34	5.40
5	5	18	11.04	5.30
6	15	3	10.99	2.96
7	15	23	11.20	5.18
8	0	3	10.93	2.75
9	10	13	11.33	4.70
10	15	8	11.27	4.36
11	10	8	11.30	4.65
12	15	13	11.29	4.40
13	20	18	11.69	5.30
14	20	3	11.42	2.70
15	10	3	11.29	3.34
16	5	23	11.71	4.80
17	10	23	11.85	5.30
18	20	8	11.52	3.90
19	0	18	11.73	4.75
20	0	23	11.93	4.58
21	5	8	11.63	4.24
22	0	13	11.87	4.26
23	20	13	11.81	4.62
24	0	8	10.66	3.70
25	15	18	11.85	5.58

APPENDIX I (cont'd)

TABLE V Mean fork length of coho developmental stages tested.

HOLDING STOCK			EXPERIMENTAL GROUPS		
Date coll.	Date meas.	Mean ± SE (cm)	Test Group	Test Period	Mean ± SD (cm)
Jul.2-Aug.20 1970	Aug.7 1970	4.70 ± 0.04	survival tests	Aug.27-Oct.31, 1970	6.65 ± 0.82 7.29 ± 0.87
- -	Nov.30 1970	7.30 ± 0.07	Gr.II adv.fry	Nov.16-Dec.30 1970	8.93 ± 0.53
- -	Mar.14 1971	9.72 ± 0.05	Gr.III pre-smolts	Mar.15-Apr.19 1971	9.65 ± 0.41
- -	May 11 1971	10.78 ± 0.03	Gr.IV smolts	May 27-June 23 1971	11.43 ± 0.49
Jul.2-14, 1971	Jul.17 1971	4.17 ± 0.04	Gr. I fry	Jul.29-Aug.25, 1971	4.95 ± 0.32
Aug.27 1971	Aug.28 1971	4.12 ± 0.04	Gr. I fry (repeat series)	Aug.26-Oct.1, 1971	5.14 ± 0.28
Aug.27 1971	Aug.28 1971	4.12 ± 0.04	Pulp mill effluent	Oct.3-15, 1971	5.29 ± 0.22

To convert fork length to total length add 7.0% to each measurement.

APPENDIX II

Effects of bleached kraft mill effluent on performance

Equal grab-samples of effluent were collected October 5, 1971, from the two main discharge pipes of the Harmac pulp mill, Nanaimo, British Columbia, and transported to the laboratory in 25-gallon barrels coated with a non-toxic lining. These were stored under refrigeration at 37°F to minimize possible chemical changes. Prior to each experiment, the required volume of bleached kraft mill effluent was prepared in a 1:1 mixture, in accordance with the normal flow volumes from the main sewers at the mill.

Using routine acclimation and test procedures previously described, swimming speeds for coho salmon fry (5.29 cm) were tested during October 7-15, 1971, in 10% bleached kraft mill effluent for both fresh and brackish water (20 ‰S) at 18C. Pilot investigations revealed that visibility in the highly coloured effluent was insufficient to conduct experiments at concentrations exceeding 10% by volume. Extended acclimation to the effluent was impractical due to the quantity needed, and biologically questionable as fish are likely to avoid such concentrations in nature. As a compromise, trials were conducted on fish exposed for 12 hours to test conditions during acclimation, prior to testing, and also on fish with no previous exposure to the effluent.

The decline in swimming capacity in the bleached kraft mill effluent mixture was significant ($P < 0.05$) for fish pre-exposed in fresh water but not at 20 ‰S. Fish tested acutely to the effluent showed no significant difference in performance from the controls in either fresh water or 20 ‰S (see table).

The results suggest that extended exposure to the effluent in fresh water may seriously reduce the swimming capacity of underyearling coho. At 20 ‰S, no difference was found, suggestive that exposure time was inadequate and/or that physiological affects of the effluent may, in some way, be buffered at intermediate salinities.

Critical swimming speeds (L/sec) for coho fry in 10‰ (by volume) bleached kraft mill effluent for fresh and estuarine waters at 18C.

FRESHWATER			20 ‰S		
Control	Acute exposure	pre-exposed	Control	Acute exposure	pre-exposed
7.18	6.60	5.46	7.00	7.26	7.00
7.08	6.00	4.78^1	6.75	7.56	6.80
7.13	6.30	5.12	6.88	7.14	6.90
t_s values	2.76 ns	6.09*		3.17 ns	0.21 ns

[1] Prior to testing, acclimation temperature was 2.5C above the required test temperature.

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