

Influence of Temperature and Current Speed on the Swimming Capacity of Lake Whitefish (*Coregonus clupeaformis*) and Cisco (*C. artedii*)¹

Louis Bernatchez and Julian J. Dodson

Département de biologie, Université Laval, Québec, Qué. G1K 7P4

Bernatchez, L., and J. J. Dodson. 1985. Influence of temperature and current speed on the swimming capacity of lake whitefish (*Coregonus clupeaformis*) and cisco (*C. artedii*). *Can. J. Fish. Aquat. Sci.* 42: 1522–1529.

We tested the influence of temperature and water velocity on metabolic rate and swimming performance of lake whitefish (*Coregonus clupeaformis*) and cisco (*C. artedii*) using respirometry techniques. Tests were conducted at 5, 12, and 17°C (speed range 20–102 cm·s⁻¹) for lake whitefish and at 12°C (speed range 20–63 cm·s⁻¹) for cisco. Fish lengths ranged from 10 to 39 cm (TL). The net aerobic cost of swimming, obtained by subtracting standard from total oxygen consumption, was twice as high for cisco as that for lake whitefish at any swimming speed. However, the standard metabolic rate of lake whitefish was almost the double that of cisco acclimated to the same temperature. Values of metabolic scope for activity coupled with the net cost of swimming showed that coregonines were not good performers compared with most salmonids. The active metabolic rate, scope for activity, and critical swimming speed for lake whitefish were maximal at 12°C and minimal at 5°C. Swimming endurance of lake whitefish decreased logarithmically with swimming speed and was reduced at low temperature, the distance traversed at any given swimming speed being minimal at 5°C. Our results support the hypothesis that the combined effect of high water velocities and low ambient temperature on coregonines' metabolism and swimming performance may be a more important factor than specific spawning temperature in the timing of the early reproductive migration of anadromous coregonines in the Eastmain River, James Bay.

Les auteurs ont testé l'effet de la température et des vitesses de courant sur le taux métabolique et la performance de nage du grand corégone (*Coregonus clupeaformis*) et du cisco du lac (*C. artedii*). Les tests ont été conduits à 5, 12 et 17°C (vitesses 20–102 cm·s⁻¹) pour le grand corégone et à 12°C (vitesses 20–63 cm·s⁻¹) pour le cisco. La longueur des poissons variait de 10 à 39 cm (LT). Le coût aérobique de nage est deux fois plus élevé pour la cisco de lac que pour le grand corégone à n'importe quelle vitesse de nage. Cependant, le métabolisme de base du grand corégone est presque le double de celui du cisco de lac acclimaté à la même température. Les valeurs de champ métabolique d'activité et du coût de locomotion démontrent que la capacité de nage des corégoninés est moindre que pour la plupart des salmonidés. Le métabolisme actif, le champ métabolique d'activité ainsi que la vitesse critique de nage du grand corégone sont maximum à 12°C et minimum à 5°C. L'endurance de nage du grand corégone diminue de façon logarithmique avec la vitesse de nage et est réduite à basse température, la distance nagée à n'importe quelle vitesse de nage étant minimale à 5°C. Les résultats supportent l'hypothèse que l'effet néfaste de basses températures sur le métabolisme et la performance de nage des corégoninés puisse être un facteur plus important que la température spécifique du frai pour le synchronisme de la migration de reproduction hâtive des corégoninés anadromes de la rivière Eastmain, Baie James.

Received February 4, 1985
Accepted May 24, 1985
(J8098)

Reçu le 4 février 1985
Accepté le 24 mai 1985

Anadromous lake whitefish (*Coregonus clupeaformis*) and cisco (*C. artedii*) enter the Eastmain River, James Bay, as early as mid-July and migrate 27 km upstream where the majority traverse 6 km of rapids from mid-August to mid-September when mean water temperatures decline from 17 to 10°C. Such an early migration results in a wait of 6–10 wk on spawning grounds without feeding prior to spawning which occurs when temperatures decline below 5°C. This represents a costly energetic penalty compared with a

hypothetical situation in which fish could remain on feeding grounds in James Bay as late as possible and migrate just in time for spawning. Neither species appears able to afford such a penalty, as they experience high winter mortality (Dodson et al. 1985) and, although iteroparous, do not spawn yearly (Morin et al. 1982), a habit related to the cost of accessory reproductive activities (e.g. migration) in poor habitats (Bull and Shine 1979). In order to explain such apparently nonadaptive behavior, we hypothesized that low temperatures and high water velocities encountered in rapids downstream of spawning grounds may represent an important environmental constraint to the migration of cisco and lake whitefish and that their influence on metabolism and swimming performance may be a major factor

¹Contribution to the program of GIROQ (Groupe Interuniversitaire de Recherches Océanographiques du Québec).

controlling the timing of the reproductive migration of both species.

The concept of optimal temperature for migration (Weihs 1984) suggests that fish could select temperatures that would lower the energy requirements of migration or increase muscular efficiency and other physiological factors related to swimming activity. Although the effect of temperature on the energy requirements at various levels of activity has been studied for several salmonids (Brett and Glass 1973; Rao 1971; Webb 1971; Beamish 1980), there are no systematic studies dealing with coregonine species. Furthermore, most studies describing the effect of temperature on swimming performance deal with the effect of temperature on critical swimming speed (Brett and Glass 1973; Griffiths and Alderdice 1972; Jones et al. 1974; Beamish 1980) which is an approximation of the maximum speeds that a fish can sustain without fatiguing (Brett 1964). Very few are concerned with the exact effect of temperature on fatigue time occurring at prolonged swimming speeds (Rulifson 1977) which are higher than critical swimming speeds and result in fatigue within 200 min to 20 s (Beamish 1978).

The active oxygen consumption, the metabolic scope for activity which represents the aerobic energy available for propulsion (Fry 1947), and the critical swimming speed are three major parameters that define the swimming capacity of fish (Beitinger and Fitzpatrick 1979). Our study was designed as a laboratory evaluation of the effect of temperature on these parameters and on fatigue time documented at prolonged swimming speeds. The swimming capacity of coregonines is compared with that of other salmonids and discussed relative to the reproductive migration exhibited by the anadromous coregonines of the Eastmain River.

Material and Methods

Swimming capacity was evaluated for lake whitefish at three temperatures (5, 12, 17°C). As only few cisco were available, experiments for these fish were conducted at 12°C for inter-specific comparisons.

Lake whitefish were reared at Glenora Fisheries Station, Ontario Ministry of Natural Resources (OMNR), from eggs obtained from wild stocks of Lake Ontario and Bay of Quinte. Fish had always been held in 600- and 2400-L circular tanks with a mean current speed of 10–15 cm·s⁻¹. Cisco were captured in Lake Simcoe, kept for 8 mo at the OMNR research laboratory in Maple, and transferred to Glenora where they were trained to swim for 3 wk before being used in experiments. Fish were fed once daily on a pelleted diet formulated for salmonids. Fish were acclimated to each experimental temperature by a change of 1.0°·d⁻¹ and held for a period of 1 wk at the desired temperature before the start of experiments. Food was withheld from fish for 24 h before experiments, thus avoiding the elevation of standard metabolism due to feeding (Beamish 1964).

Two types of respiration chambers were used for the experiments. The respirometer used for fish >320 g was described in detail by Farmer and Beamish (1969); the water is driven by a centrifugal pump into an expansion chamber provided with turbulence grids and then through a reduction cone resulting in microturbulent flow and minimum velocity differences from the walls to the center of the chamber in which the fish are forced to swim when necessary by a mild electrical shock of 3–9 V (60-cycle ac). The volume of the chamber is 168 L. Four modified Blazka-type respirometers (Waiwood and Beamish 1978) of 3.2 L were used for experiments with cisco and lake

whitefish <20 g. In all experiments, temperature was controlled within ±0.2°. Cross-sectional area of the fish never exceeded 10% of that of the swimming chambers so that no correction for the volume effect was necessary (Smit et al. 1971).

Oxygen Consumption

Experiments were conducted on three groups of fish: (1) 16 large lake whitefish of the size of adult fish in the Eastmain River (mean weight of 364 ± 39 g (SD), mean total length of 34.2 ± 1.1 cm); (2) 8 small lake whitefish (15.0 ± 2.9 g, 12.7 ± 0.7 cm); (3) 8 cisco (18.9 ± 2.7 g, 13.5 ± 0.5 cm). For experimental groups 2 and 3, one fish was chosen at random and placed in the respirometer at least 12 h before an experiment and forced to swim against a current of 20 cm·s⁻¹ in order to avoid high oxygen consumption due to excitement (Brett 1964). For experimental group 1, a training period of 30–60 min was sufficient, as excitement or excessive oxygen consumption was never observed. During the training period, the respirometer was supplied with a flow of oxygen-saturated water. Water samples for oxygen measurements were taken prior to stopping the inflow of water for a period of 30 min in the large respirometer and 60 min in the Blazka respirometers. We observed that oversaturation, resulting in release of gas into the water, caused underestimation of oxygen consumption following 60 min in the large chamber. This problem was avoided by adopting a 30-min period. Oxygen concentrations were measured after this period, the current speed was increased by 10 cm·s⁻¹ for group 1 and 5 cm·s⁻¹ for groups 2 and 3, and the chamber was flushed for 15 min with oxygen-saturated water. This procedure was repeated until the fish did not swim despite electrical stimulation. The oxygen level never fell below 80% saturation. For each experiment, a similar procedure was followed but without an experimental subject to evaluate oxygen consumption not attributable to the fish. The values obtained were subtracted from values obtained in the presence of fish to obtain exact measurements of oxygen consumption. Oxygen consumption was determined by the sodium azide modification of the Winkler method.

The relationship between oxygen consumption and body weight was determined by linear regression analysis for lake whitefish at three swimming speeds (20, 30, 40 cm·s⁻¹) in order to predict the rate of oxygen consumption of fish of different sizes. Too few small lake whitefish swam at speeds >40 cm·s⁻¹ to allow regression analysis. Previous studies (Farmer and Beamish 1969; Rao 1968; Brett 1965a) have shown that the slope of this relationship varies among species and swimming speeds. However, as the slopes of these relationships for speeds <40 cm·s⁻¹ in the case of lake whitefish are almost identical to those of rainbow trout (*Salmo gairdneri*) (Rao 1968), slopes obtained by Rao (1968) for speeds at and above 50 cm·s⁻¹ were applied to lake whitefish (Table 1). Size range for cisco was too small to allow regression analysis. Thus, slopes obtained for lake whitefish were used to estimate the rate of oxygen consumption of cisco of reproductive size (280 g) in the Eastmain River.

Critical swimming speed, active oxygen consumption, and metabolic scope for activity were all derived from oxygen consumption – swimming speed experiments. Critical swimming speed was determined for each fish tested using the formula elaborated by Brett (1964):

$$C = V + (t \cdot \Delta t^{-1}) \Delta v$$

where C is the critical swimming speed (centimetres per second),

TABLE 1. Regression equations of the logarithm of oxygen consumption (Y) on the logarithm of body weight (X) for lake whitefish; weight range of 12–405 g at each swimming speed (n = number of observations pooled to calculate the regressions; r^2 = correlation coefficient).

| Swimming speed ($\text{cm} \cdot \text{s}^{-1}$) | Regression equation | n | r^2 |
|--|------------------------|---------------|-------|
| 20 | $Y = 0.8657X - 0.6766$ | 16 | 0.968 |
| 30 | $Y = 0.9131X - 0.5767$ | 16 | 0.977 |
| 40 | $Y = 0.8618X - 0.3586$ | 14 | 0.987 |
| 50 | $Y = 0.8982X - 0.3496$ | From Rao 1968 | |
| 60 | $Y = 0.9337X - 0.2235$ | From Rao 1968 | |
| 70 | $Y = 0.9916X - 0.2146$ | From Rao 1968 | |

Δt is the prescribed period of time (min), Δv is the velocity increment (centimetres per second), t is time that the fish swam at the last speed (min), and v is the highest velocity maintained for the prescribed incremental period (centimetres per second). Active oxygen consumption corresponded to oxygen consumption predicted by the oxygen consumption – swimming speed equation at critical swimming speed. The scope for activity was obtained by subtracting the standard metabolic rate, measured by extrapolation of the oxygen consumption – swimming speed relationship to zero activity, from the active metabolic rate.

Fatigue Time

Time to fatigue was determined at two temperatures (5, 12°C) for lake whitefish and only at 12°C for cisco. Tests were conducted in the 168-L chamber using the method of fixed velocity described by Brett (1967). A series of velocities was chosen ranging from swimming speeds at which fish did not fatigue within 180 min to the maximum speed of $1.02 \text{ m} \cdot \text{s}^{-1}$ that could be reached by the respirometer. Fish were placed in the chamber at low velocity ($20\text{--}30 \text{ cm} \cdot \text{s}^{-1}$) for a 20- to 30-min conditioning period. The velocity was raised to an intermediate level for 30 s and then increased to the prescribed velocity. The fish were kept from resting by mild electrical shocks. The experiments were conducted with only one fish at a time in the chamber for group 1; groups of 5–10 fish were used for groups 2 and 3. As a fish fatigued (when it did not swim despite electrical shocks) it was removed from the chamber with forceps. The 50% time to fatigue for each experiment was determined by the method of probit analysis (Finney 1971). Previous studies (Brett 1967; Beamish 1980) showed that this method provided a good measure of fish endurance despite erratic behavior.

Results

Oxygen Consumption – Swimming Speed Relationships

The oxygen consumption – swimming speed relationships for lake whitefish demonstrate that the rate of increase in oxygen consumption with speed decreases with temperature, the slope at 5°C being the double of those obtained at 12 and 17°C (Fig. 1; Table 2). Analysis of covariance performed on slopes at 5, 12, and 17°C revealed significant differences ($p < 0.05$). An a posteriori SNK test (Student–Newman–Keuls) (Zar 1974) revealed that the slope at 5°C differs significantly from slopes at 12 and 17°C ($p < 0.05$). Although the value of the slope at 17°C is lower than at 12°C, they do not differ significantly ($p > 0.05$).

The rate of increase in oxygen consumption with speed for cisco (280 g) at 12°C is greater than that for lake whitefish

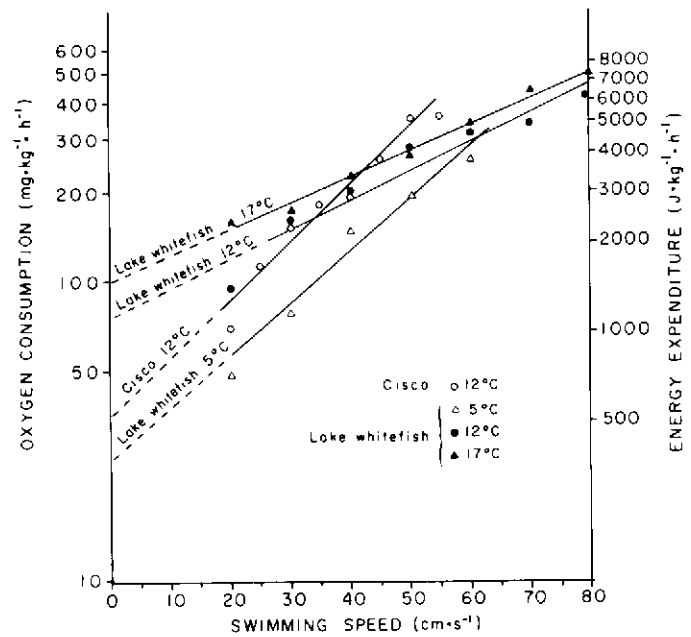


FIG. 1. Oxygen consumption and energy expenditure in relation to swimming speed and temperature for lake whitefish of 364 g (34 cm TL) and cisco corrected to correspond to a weight of 280 g (29 cm TL). Regression lines end at the maximum speed tested. The standard rate of oxygen consumption is determined by extrapolation (broken lines) to zero activity.

(364 g) tested at the same temperature (t -test, slopes, $p < 0.05$) but does not differ from that for lake whitefish acclimated and tested at 5°C (t -test, slopes, $p > 0.05$). Standard metabolic rate, obtained by extrapolation to zero activity, is much lower for cisco than for lake whitefish at the same temperature (Fig. 1; Table 2).

Figure 2 illustrates the aerobic cost of swimming calculated at different swimming speeds for cisco and lake whitefish and compared with other salmonids. Regression slopes (Table 1) were used for adjusting oxygen consumption to a weight of 100 g for the comparison.

Standard metabolic rate of lake whitefish increases with temperature (Table 3), being 4 times higher at 17 than at 5°C. Active metabolic rate is maximal at 12°C. The difference in active metabolic rate is more pronounced between 5 and 12°C than between 12 and 17°C. Similarly, the metabolic scope for activity (obtained by subtraction of the standard from the active metabolic rate) and the critical swimming speed are maximal at 12°C and minimal at 5°C. An a posteriori SNK test revealed a significant difference between 5 and 12°C ($p < 0.05$) in critical swimming speeds.

Fatigue Time

Lake whitefish fatigue faster at 5 than at 12°C (Table 4). Swimming endurance of lake whitefish decreased logarithmically with increased swimming speed at both temperatures and for both sizes (Fig. 3). The slope of the relationship is the same for the 364-g lake whitefish at 5 and 12°C. The swimming endurance, in terms of fatigue time at a given swimming speed, is much better for small than for large lake whitefish at 12°C. Small cisco and lake whitefish of comparable weight swimming at $63 \text{ cm} \cdot \text{s}^{-1}$ exhibit no significant difference in fatigue time at 12°C (Table 4). In terms of body length, however, cisco may fatigue faster than whitefish of the same length (Fig. 3). Further-

TABLE 2. Regressions of the logarithm of energy expenditure (Y) on the swimming speed (X) for cisco and lake whitefish at each weight and temperature (n = number of observations pooled to calculate the regressions; F = F -value for the significance of regression; p = probability level of significance; r^2 = correlation coefficient).

| Species | Temperature (°C) | Weight (g) | No. of fish | Regression equation | n | F | p | r^2 |
|-------------------------------|------------------|------------|-------------|-----------------------|-----|--------|--------|-------|
| <i>Coregonus artedii</i> | 12 | 18.9 | 8 | $Y = -1.618 + 4.396X$ | 43 | 207.85 | <0.001 | 0.84 |
| | | 280 | | $Y = -1.919 + 4.396X$ | | | | |
| <i>Coregonus clupeaformis</i> | 5 | 364 | 8 | $Y = -2.444 + 4.237X$ | 36 | 102.33 | <0.001 | 0.75 |
| | 12 | 364 | 10 | $Y = -1.158 + 2.198X$ | 50 | 230.73 | <0.001 | 0.83 |
| | 17 | 364 | 9 | $Y = -0.867 + 2.023X$ | 44 | 179.03 | <0.001 | 0.81 |

TABLE 3. Metabolic rates and critical swimming speeds for lake whitefish (364 g) at three acclimation temperatures and for cisco (18.9 g). Standard metabolism, active metabolism, and scope for activity are given with the 95% confidence limits.

| Species | Temperature (°C) | Standard metabolism (mg O ₂ ·kg ⁻¹ ·h ⁻¹) | Active metabolism (mg O ₂ ·kg ⁻¹ ·h ⁻¹) | Critical swimming speed ± SD (cm·s ⁻¹) | Metabolic scope for activity (mg O ₂ ·kg ⁻¹ ·h ⁻¹) |
|-------------------------------|------------------|---|---|--|--|
| <i>Coregonus clupeaformis</i> | 5 | 19 < 26 < 36 | 238 < 293 < 360 | 63.0 ± 6.0 | 219 < 267 < 324 |
| | 12 | 66 < 77 < 89 | 365 < 403 < 445 | 75.0 ± 9.5 | 299 < 326 < 356 |
| | 17 | 85 < 100 < 116 | 355 < 387 < 421 | 67.4 ± 4.4 | 270 < 287 < 307 |
| <i>Coregonus artedii</i> | 12 | 34 < 44 < 57 | 345 < 380 < 419 | 45.8 ± 8.1 | 311 < 336 < 362 |

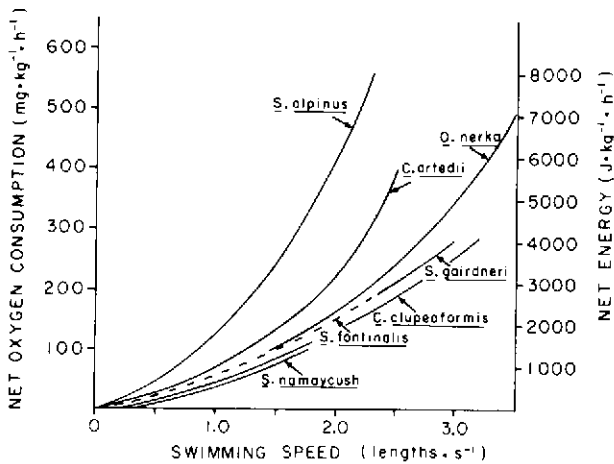


FIG. 2. Net oxygen and energy requirements for a given swimming speed calculated by subtraction of standard from total metabolic rate for lake whitefish and cisco. All values are based on a standard weight of 100 g. Data for arctic char (*Salvelinus alpinus*), brook trout (*S. fontinalis*), and lake trout (*S. namaycush*) are from Beamish (1980). Those for sockeye salmon (*O. nerka*) and rainbow trout (*Salmo gairdneri*) are respectively from Brett and Glass (1973) and Rao (1971). Note that *S. fontinalis* and *S. gairdneri* correspond to the same curve.

more, only two lake whitefish died during 68 trials, while 12 of the 20 cisco tested died within 48 h following the experiments.

All 364-g lake whitefish tested (64 trials) that could swim longer than 75 min did not fatigue within the experimental period, and all 14-g lake whitefish (68 trials) that could swim longer than 30 min did not fatigue. Median critical swimming speed (Fig. 4), which is an approximation of maximum sustained speed (Brett 1964), is identical to the speed corresponding to maximum fatigue time for 14-g lake whitefish, suggesting

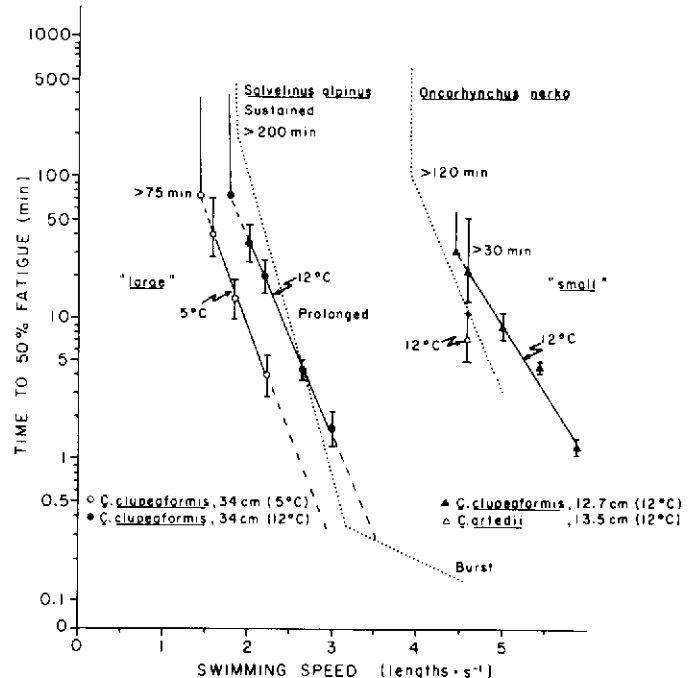


FIG. 3. Relationship between time to 50% fatigue and swimming speed (lengths·s⁻¹) for lake whitefish and cisco. Horizontal lines indicate 95% confidence intervals. Only one swimming speed could be tested for cisco. Sustained swimming speeds are represented by velocities that could be maintained without fatigue for more than 75 min for 34-cm lake whitefish and more than 30 min for the 12.7-cm lake whitefish. Broken lines represent extrapolations of the fatigue time – swimming speed relationship. The relationship between time to 50% fatigue and swimming speed for *S. alpinus* (34 cm) and *O. nerka* (13.5 cm) were determined by Beamish (1980) and Brett (1967), respectively. Note that smaller fish can swim relatively faster than large fish.

TABLE 4. Relation of swimming speed to the 50% fatigue time for lake whitefish and cisco as estimated by probit analysis. Maximum test time was 180 min. The 50% fatigue time is given with the 95% confidence interval.

| Species | Weight (g) | Temperature (°C) | Swimming speed | | No. of fish tested | 50% fatigue time (min) |
|-------------------------------|------------|------------------|--------------------|------------------------|--------------------|------------------------|
| | | | cm·s ⁻¹ | length·s ⁻¹ | | |
| <i>Coregonus clupeaformis</i> | 364 | 5 | 55 | 1.6 | 8 | 28.0 < 39.3 < 76.7 |
| | | | 63 | 1.8 | 9 | 10.3 < 14.2 < 19.2 |
| | | | 75 | 2.2 | 10 | 2.8 < 3.9 < 5.2 |
| | 14.9 | 12 | 68 | 2.0 | 10 | 25.1 < 33.3 < 46.6 |
| | | | 75 | 2.2 | 10 | 13.6 < 20.0 < 32.7 |
| | | | 90 | 2.6 | 10 | 3.6 < 4.2 < 4.9 |
| | | | 102 | 3.0 | 7 | 0.8 < 1.6 < 2.3 |
| | | | 59 | 4.6 | 20 | 13.2 < 21.3 < 55.7 |
| | | | 63 | 5.0 | 20 | 7.1 < 8.7 < 11.3 |
| 18.9 | 12 | 69 | 5.4 | 20 | 4.2 < 4.5 < 4.9 | |
| | | 74 | 5.8 | 8 | 1.1 < 1.2 < 1.4 | |
| | | 63 | 4.7 | 20 | 5.0 < 7.3 < 11.2 | |
| | | | | | | |

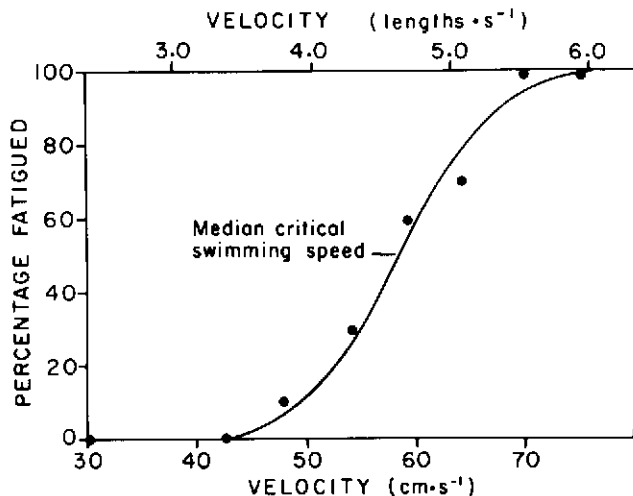


FIG. 4. Percentage of 12.7-cm lake whitefish fatigued within 120 min at 12°C when forced to swim at the velocity indicated. The velocity at which 50% of the fish tested fatigued corresponds to the median critical swimming speed (Brett 1964).

that maximum fatigue time obtained here (30 min) probably corresponds to the point of inflexion between sustained and prolonged swimming speed (Fig. 3).

Discussion

Oxygen Consumption – Swimming Speed Relationships

The rate of increase in oxygen consumption that occurs as lake whitefish swim faster is greatest at low temperatures (Table 2). Thus, including energy expenditures due to standard metabolism, swimming cost is less at 5 than at 12°C at low swimming speeds (Fig. 1). The temperature effect is less pronounced at higher speeds; at 63 cm·s⁻¹ (1.84 lengths·s⁻¹), the cost of swimming is the same at both temperatures (Fig. 1). These results agree with Brett (1964) who observed that the cost of swimming at high sustained swimming speeds is independent of temperature. However, after extrapolation of the energy expenditure – swimming speed relationship at 5°C (Fig. 1) beyond the critical swimming speed (63 cm·s⁻¹), we suggest that the cost

of swimming would be higher than at 12 and 17°C. Although the energy required for swimming at speeds higher than critical comes partly from anaerobic metabolism (Beamish 1980), such extrapolation is justified, as the relationship between the power needed for propulsion and swimming speed will remain constant, being independent of the energy fuel (Jones 1982).

The values of regression coefficients for the oxygen consumption – swimming speed relationship we obtained are comparable with those for other salmonids (Beamish 1978, 1980). Regression coefficients calculated from Brett and Glass (1973, fig. 3) for sockeye salmon vary from 3.16 to 1.77 at 5 and 20°C, respectively, a twofold decrease as observed in this study for lake whitefish of comparable size. Rao (1968) also obtained a decrease in regression coefficients between 5 and 17°C in rainbow trout, but Beamish (1980) did not find any temperature effect for arctic char (*Salvelinus alpinus*). A possible explanation for the rate of increase in oxygen consumption being higher at low temperature is the increase of drag associated with decreasing temperatures. Weihs (1984) stated that water viscosity is 30% greater at 10 than at 20°C. As the drag that the fish must overcome is augmented by the same ratio, more energy is required for motion in colder waters. Since standard metabolism is lower at low temperatures, the rate of increase of oxygen consumption must be greater to furnish the increasing energy demands of swimming faster in cold water. However, this explanation does not apply to arctic char. Results obtained for that species suggest an increase of aerobic muscle efficiency (Webb 1971; Jones 1982) with decreasing temperature.

The net energy requirements for swimming of cisco and lake whitefish are in the range obtained for other salmonids (Fig. 2), although energy requirements for cisco are particularly high, being about twice that for most salmonids. Only the arctic char is less efficient, with a net energy requirement for swimming about three times greater than for other salmonids. Such differences in the net cost of locomotion among closely related species are surprising if one considers that the power needed for propulsion equals the drag that the fish has to overcome and that the shape of the fish and its locomotion mode are the main factors affecting the drag (Webb 1975). These observations contradict the model elaborated by Schmidt-Nielsen (1972) predicting the cost of swimming for fish. According to this model, the cost of swimming is surprisingly similar among

TABLE 5. Standard metabolic rate and scope of activity for different salmonids. Values are calculated for a standard weight of 100 g using an exponent of 0.8 (Basu 1959).

| Species | Temperature (°C) | Standard rate (mg O ₂ ·kg ⁻¹ ·h ⁻¹) | Metabolic scope for activity (mg O ₂ ·kg ⁻¹ ·h ⁻¹) | Reference |
|-----------------------------|------------------|---|--|----------------------|
| <i>Coregonus artedii</i> | 12 | 43 | 287 | Present study |
| <i>Salvelinus namaycush</i> | 15 | 46 | 187 | Beamish 1980 |
| <i>S. fontinalis</i> | 15 | 57 | 427 | Beamish 1980 |
| <i>Oncorhynchus nerka</i> | 12 | 62 | 725 | Brett and Glass 1973 |
| <i>S. alpinus</i> | 15 | 80 | 651 | Beamish 1980 |
| <i>C. clupeaformis</i> | 12 | 91 | 309 | Present study |
| <i>C. autumnalis</i> | 7.2 | 109 | | Wohlschlag 1957 |
| <i>S. gairdneri</i> | 15 | 114 | 472 | Rao 1968 |
| <i>C. sardinella</i> | 10 | 127 | | Wohlschlag 1957 |

different teleosts, from the sockeye salmon (*Oncorhynchus nerka*) known as a very efficient swimmer (Brett 1965b), to the European eel (*Anguilla anguilla*), known as being relatively inefficient from a hydromechanical point of view (Weihs 1984). Muscle and propellor efficiency (Webb 1971) must be much more important than has been considered to date.

Swimming Capacity Parameters

Critical swimming speeds obtained here for lake whitefish are considerably higher than the value of 52 cm·s⁻¹ found in an earlier study of lake whitefish of the same size (Jones et al. 1974). In that case, wild fish were used and were not trained to swim against a current as in the present study. Furthermore, the combination of increment of time (10 min) and velocity increase (10 cm·s⁻¹) used in evaluating critical swimming speed was different from that recommended by Brett (1964) and the ones we used. As changes in parameter values will alter the estimation of critical swimming speed (Farlinger and Beamish 1977), our results are not readily comparable with those of Jones et al. (1974).

Metabolic scopes of coregonines fall within the range of those for other salmonids (Table 5). The scope for activity of lake whitefish is higher than that obtained for cisco of the same weight. Values of metabolic scope for activity coupled with the net cost of swimming (Fig. 2) show that coregonines are not good performers compared with most salmonids, especially in the case of cisco which has one of the lowest scopes for activity and one of the highest costs of swimming.

Cisco have the lowest standard metabolic rate of salmonids studied and lake whitefish one of the highest (Table 5). The difference in metabolic rates obtained for cisco and lake whitefish may be partly related to the fact that they were tested in different apparatus because of size differences. This could be due to different velocity profiles in the respirometers. This, however, was not tested. Nevertheless, the use of different respirometers for comparative studies seems a common practice (e.g. Beamish 1980) and is considered acceptable.

Optimal temperature as defined by Fry (1947) is the temperature at which an animal can best perform a certain activity. For the lake whitefish, the critical swimming speed, the metabolic scope for activity, and the maximum oxygen consumption are maximal at 12°C compared with 15°C for most salmonids (Beamish 1980). This suggests that the optimal temperature for swimming activity of coregonines is lower than that of other salmonids.

Fatigue Time

Although cisco appear to fatigue faster than lake whitefish of the same length and exhibit greater mortality due to fatigue, the data are too limited to conclude that cisco swimming endurance is significantly less than that of lake whitefish. Thus, we assume that fatigue time obtained for lake whitefish represents a best estimate of cisco swimming endurance.

Lake whitefish swimming endurance is clearly affected by temperature (Fig. 3). Rulifson (1977) also found that time before fatigue increases with temperature for three species of estuarine fish and probably reflects the effect of acute temperature on biochemical reaction rate (Sidell 1980). The logarithmic relationship between time to 50% fatigue and relative swimming speed is quite similar to that obtained for arctic char (Beamish 1980) and sockeye salmon (Brett 1964) (Fig. 3). The main difference is the time at which the swimming mode switches from sustained to prolonged due to the changes in biochemical processes which supply fuel for their application. Beamish (1978) suggested that this time should be fixed at 200 min. Our results show that it can be lower than 200 min and varies with size. Brett (1967) found that it could vary from 120 min for a 14-cm sockeye salmon up to 500 min for a 53.2-cm fish, suggesting that the time at which swimming mode switches from sustained to prolonged varies between species and size and should be evaluated in each case. This is important if one wants to establish the fatigue time curve correctly and make realistic predictions for ecological applications. For example, taking 200 min for a 14-g lake whitefish at 12°C (Fig. 3) would underestimate the maximum sustained swimming speed (3.6 lengths·s⁻¹ rather than the observed 4.4 lengths·s⁻¹).

Maximum sustained swimming speed observed at 12°C in fatigue time experiments (65 cm·s⁻¹) is considerably lower than the critical swimming speed (75 cm·s⁻¹) evaluated from Brett's equation at the same acclimation temperature. Thus, calculated critical swimming speed overestimated the maximum sustained swimming speed in the present study.

Calculation of maximum distance traversable before fatigue at different water velocities and temperatures can be made from the determination of swimming performance (Fig. 5). At low water speeds, distance traversed before fatigue is maximal by choosing low swimming speeds. At intermediate water speeds, e.g. 75 cm·s⁻¹, there is an intermediate swimming speed that maximizes distance traversed. Fish can swim much longer at 12 than at 5°C. For instance, at a water velocity of 25 cm·s⁻¹, lake whitefish swimming at 70 cm·s⁻¹ will swim 1000 m before

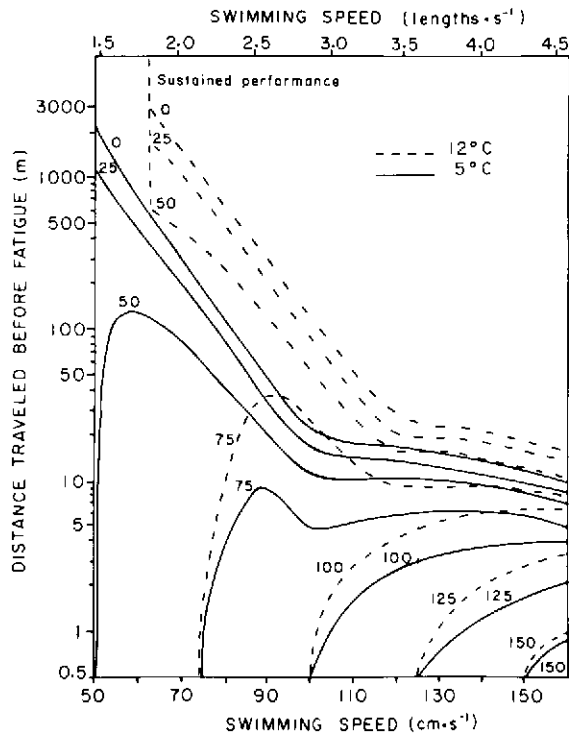


FIG. 5. Effect of temperature on the maximum distance traveled over ground before fatigue, predicted for a 34-cm lake whitefish swimming at different speeds against different water velocities. Each curve represents performance in water current of a given velocity. The distances were calculated from the relationships between 50% fatigue and prolonged swimming speeds obtained in Fig. 3. Distances traveled at burst speeds (>2.9 lengths \cdot s $^{-1}$ at 5°C, >3.5 lengths \cdot s $^{-1}$ at 12°C) were calculated from the relationship obtained for *S. alpinus* by Beamish (1980) and *S. gairdneri* by Bainbridge (1960). Both relationships gave the same result.

exhaustion at 12°C and no more than 200 m at 5°C. The effect of temperature on distance traversed over ground is more pronounced at low swimming speeds.

Ecological Considerations

In the context of fish migration, water velocity and temperature will affect the maximum distance that a fish in a river can traverse before experiencing exhaustion and finding a resting point. In a theoretical approach, Priede (1977) discussed the natural selection for energetic efficiency and the relationship between activity level and mortality. The model, derived from sonic tracking observations on brown trout (*Salmo trutta*), makes predictions as to the potential mortality rate associated with a given level of activity. Predictions of the potential mortality are based on the fact that any animal must function within its scope of activity (Fry 1947). Enforced activity above the limit of scope causes disturbance of homeostasis implying a certain death. For instance, Wood et al. (1977) showed that exhausting activity results in a marked and immediate drop in blood pH that eventually limits vital metabolic reactions, causes problems of oxygen delivery, and decreases myocardial contractility. Such problems must be avoided if one considers the low buffering capacity of fish (Jones and Randall 1978). Thus, increased time spent above the active metabolic rate may be an important stress and mortality factor in natural populations. Priede's model predicts for the brown trout that an increase of

TABLE 6. Length and mean velocity of the rapids that cisco and lake whitefish have to traverse to get to the spawning grounds. Mean velocity corresponds to the mean time for 10 drogues to descend the given distance for each series of rapids, Eastmain River, 1983.

| Rapids | Length (m) | Velocity \pm SD ($\text{m} \cdot \text{s}^{-1}$) |
|--------|------------|--|
| 1 | 257 | 1.20 \pm 0.05 |
| 2 | 86 | 1.52 \pm 0.20 |
| 3 | 200 | 1.05 \pm 0.08 |
| 4 | 430 | 0.66 \pm 0.02 |
| 5 | 50 | 1.41 \pm 0.20 |
| 6 | 100 | 1.18 \pm 0.06 |
| 7 | 450 | 1.07 \pm 0.02 |

the daily time spent at 99% of the active metabolic rate from 0.18 to 0.2% would increase the potential mortality rate by 29% although the increase of energy expenditure is only 0.004% of the total expenditure of the fish. Salmonids that migrate in rivers with rapids probably spend important daily periods of time at levels of activity above the active metabolic rate in order to traverse zones of high velocities, although this has never been documented. Thus, according to Priede's model, one may assume that any factor that would lead to a reduction of time spent above the active metabolic rate during the migration would be of great advantage to the migrating fish.

Selecting zones of lower water velocities certainly represents such a factor. Osborne (1961) observed that chinook salmon (*Oncorhynchus tshawytscha*) during their upstream migration in rivers make use of the shape of the bottom topography to move through zones of lower local water velocity, thus augmenting distance traversed before exhaustion. Brett (1965b) also reported that the mean water velocity of the Fraser River is higher than the mean migration speed of sockeye salmon evaluated from energy expenditure for migration, suggesting that salmon are highly efficient in finding zones of lower water velocity. Coregonines of the Eastmain River have to traverse seven sections of rapid water to get to the spawning grounds (Table 6). However, from calculations in Fig. 5, it is evident that mean current speed in the rapids is too elevated for coregonines to be able to traverse any of the sections entirely before fatigue at any temperature. This suggests that migrating coregonines must select zones of low water velocities and have to swim actively from one rest point to another.

Avoiding low water temperature during migration may be another factor that would reduce time spent above the exhaustion level. Present results show that coregonines can swim longer distances before fatigue at 12 than at 5°C. Thus, migrating at 12 instead of 5°C would decrease the time spent above the exhaustion level during the migration in the rapids. Although the effect of temperature is less pronounced at high velocities (Fig. 5), it should not be neglected. For instance, distance traveled before fatigue at a current speed of 125 $\text{cm} \cdot \text{s}^{-1}$ is still 33% greater at 12 than at 5°C. Time spent above exhaustion level during the migration is then reduced by the same ratio. According to Priede's model, migrating at 12 compared with 5°C would greatly decrease potential mortality during the migration. Migrating at low temperatures could also result in an additional penalty by extending the time needed for migration through the rapids. Brett (1964) showed that the time

of recovery for oxygen debt repayment following exhaustion permitting successful reperformance was 191 ± 3.8 min and independent of temperature for sockeye salmon. Wood et al. (1977) demonstrated that a mean period of 6 h was necessary to recover from acidosis following an exhausting activity in flounder (*Platichthys stellatus*). In the case of coregonines in the Eastmain River, avoiding low temperatures would decrease the number of such recovery periods, thus reducing the time spent in the rapids where they are susceptible to predation by northern pike (*Esox lucius*), which are abundant in the Eastmain River (L. Bernatchez, unpubl. data).

We have provided evidence that low temperatures lead to poor swimming capacity by diminishing maximum oxygen uptake and the metabolic scope for activity, resulting in a decrease in distance traversed before fatigue at any swimming speed. This may in turn lead to an increase in potential mortality by augmenting the time at which migrating fish will swim above exhaustion level. Although other important factors may be involved, our results support the hypothesis that the effect of low ambient temperature on coregonine swimming capacity associated with high water velocities may be a more important factor than the specific spawning temperature in the timing of the reproductive migration of coregonines in the Eastmain River.

Acknowledgments

We gratefully acknowledge Mr. J. W. Christie, Director, Glenora Research Station, OMNR, who provided facilities and the lake whitefish for this study; Dr. D. Evans, Maple Research Station, OMNR who provided the cisco, and Dr. F. W. H. Beamish, University of Guelph, for providing the respirometers and valuable advice during the experiments. This research was funded by an NSERC grant to J.J.D.; L.B. was funded by an FCAC (Québec) postgraduate scholarship.

References

- BAINBRIDGE, R. 1960. Speed and stamina in three fish. *J. Exp. Biol.* 37: 129-153.
- BASU, S. P. 1959. Active respiration of fish in relation to ambient concentrations of oxygen and carbon dioxide. *J. Fish. Res. Board Can.* 16: 175-212.
- BEAMISH, F. W. H. 1964. Respiration of fishes with special emphasis on standard oxygen consumption II. Influence of weight and temperature on respiration of several species. *Can. J. Zool.* 42: 177-188.
1978. Swimming capacity, p. 101-187. In W. S. Hoar and J. D. Randall [ed.] *Fish physiology*. Vol. 7. Academic Press, New York, NY.
1980. Swimming performance and oxygen consumption within the genus *Salvelinus*, p. 739-748. In E. K. Balon [ed.] *Charrs: salmonid fishes of the genus Salvelinus*. Dr. W. Junk Publishers, The Hague.
- BEITINGER, T. L., AND L. C. FITZPATRICK. 1979. Physiological and ecological correlates of preferred temperatures in fish. *Am. Zool.* 19(1): 319-329.
- BRETT, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* 21: 1183-1226.
- 1965a. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Board Can.* 22: 1491-1501.
- 1965b. The swimming energetics of salmon. *Sci. Am.* 213: 80-85.
1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. *J. Fish. Res. Board Can.* 24: 1731-1741.
- BRETT, J. R., AND N. R. GLASS. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J. Fish. Res. Board Can.* 30: 379-387.
- BULL, J. J., AND R. SHINE. 1979. Iteroparous animals that skip opportunities for reproduction. *Am. Nat.* 114: 296-316.
- DODSON, J. J., Y. LAMBERT, AND L. BERNATCHEZ. 1985. Comparative migratory and reproductive strategies of the sympatric anadromous coregonine species of James Bay. In M. A. Rankin [ed.] *Migration: mechanisms and adaptive significance*. *Contrib. Mar. Sci. Suppl.* 27. (In press)
- FARLINGER, S., AND F. W. H. BEAMISH. 1977. Effects of time and velocity increments on the critical swimming speed of largemouth bass (*Micropterus salmoides*). *Trans. Am. Fish. Soc.* 106: 436-439.
- FARMER, G. J., AND F. W. H. BEAMISH. 1969. Oxygen consumption of *Tilapia nilotica* in relation to swimming speed and salinity. *J. Fish. Res. Board Can.* 26: 2807-2821.
- FINNEY, D. J. 1971. Probit analysis; a statistical treatment of the sigmoid response curve. University Press, Cambridge. 272 p.
- FRY, F. E. J. 1947. Effects of the environment on animal activity. *Univ. Toronto Stud. Biol. Ser.* 55: 1-62.
- GRIFFITHS, J. S., AND D. F. ALDERDICE. 1972. Effects of acclimation and acute temperature experience on the swimming speed of juvenile coho salmon. *J. Fish. Res. Board Can.* 29: 251-264.
- JONES, D. R. 1982. Anaerobic exercise in teleost fish. *Can. J. Zool.* 60: 255-258.
- JONES, D. R., J. W. KICENIUK, AND O. S. BAMFORD. 1974. Evaluation of the swimming performance of several fish species from the Mackenzie River. *J. Fish. Res. Board Can.* 31: 1641-1647.
- JONES, D. R., AND J. D. RANDALL. 1978. The respiratory and circulatory systems during exercise, p. 425-492. In W. S. Hoar and D. J. Randall [ed.] *Fish physiology*. Vol 7. Academic Press, New York, NY.
- MORIN, R., J. J. DODSON, AND G. POWER. 1982. Life history variations of anadromous cisco (*Coregonus artedii*), lake whitefish (*C. clupeaformis*), and round whitefish (*Prosopium cylindraceum*) populations of eastern James-Hudson Bay. *Can. J. Fish. Aquat. Sci.* 39: 958-967.
- OSBORNE, M. F. M. 1961. Hydrodynamic performance of migratory salmon. *J. Exp. Biol.* 38: 365-390.
- PRIEDE, J. G. 1977. Natural selection for energetic efficiency and relationship between activity level and mortality. *Nature (Lond.)* 267: 610-611.
- RAO, R. M. M. 1968. Oxygen consumption of rainbow trout (*Salmo gairdneri*) in relation to activity and salinity. *Can. J. Zool.* 46: 781-786.
1971. Influence of activity and salinity on the weight-dependent oxygen consumption of the rainbow trout (*Salmo gairdneri*). *Mar. Biol.* 8: 205-212.
- RULIFSON, R. A. 1977. Temperature and water velocity effects on the swimming performance of young-of-the-year striped mullet (*Mugil cephalus*), spot (*Leiostomus xanthurus*), and pinfish (*Lagodon rhomboides*). *J. Fish. Res. Board Can.* 34: 2316-2322.
- SCHMIDT-NIELSEN, K. 1972. Locomotion: energy cost of swimming, flying and running. *Science (Wash., DC)* 177: 222-228.
- SIDELL, B. D. 1980. Response of goldfish muscle to acclimation temperature, alterations in biochemistry and proportions of different fiber types. *Physiol. Zool.* 53: 98-107.
- SMIT, H. J. M., J. VUJVERBERG, AND J. C. VAN VAUPEL-KLEIN. 1971. Oxygen consumption and efficiency of swimming goldfish. *Comp. Biochem. Physiol.* A 39: 1-28.
- WAIWOOD, K. G., AND F. W. H. BEAMISH. 1978. Effects of copper, pH and hardness on the critical swimming performance of rainbow trout (*Salmo gairdneri* Richardson). *Water Res.* 12(8): 611.
- WEBB, P. W. 1971. The swimming energetics of trout. II Oxygen consumption and swimming efficiency. *J. Exp. Biol.* 55: 521-540.
1975. Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Board Can.* 190: 158 p.
- WEIHS, D. 1984. Bioenergetic considerations in fish migration, p. 487-508. In J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill [ed.] *Mechanisms of migration in fishes*. Plenum Publishing Corporation, New York, NY.
- WOHLSCHLAG, D. E. 1957. Differences in metabolic rates of migratory and resident freshwater forms of an arctic whitefish. *Ecology* 38(3): 502-510.
- WOOD, C. M., B. R. MCMAKON, AND D. G. McDONALD. 1977. An analysis of changes in blood pH following exhausting activity in the starry flounder (*Platichthys stellatus*). *J. Exp. Biol.* 69: 173-185.
- ZAR, J. H. 1974. *Biostatistical analysis*. Prentice-Hall, Inc., Englewood Cliffs, NJ. 620 p.