

Relationship between Bioenergetics and Behavior in Anadromous Fish Migrations¹

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Minimizing energetic cost per unit distance is often considered the major criterion that anadromous migrants seek to optimize during upstream migration. To test this theory, we documented energetic expenditures and travel speeds of 15 anadromous fish populations involving 9 species observed during their upstream migration. Parameters that characterized fish migratory behavior and the spawning river were calculated for each population. In most cases, cost per unit distance is not minimized and migratory strategy does not conform to the theoretical optimum. Populations that make long or difficult migrations are more efficient in their use of energy reserves than populations that make shorter migrations. Only populations that need all their energy to complete the migration swim at speeds that approach the theoretical optimum. Migration length may lead to improved migratory efficiency by selecting for larger body size, more accurate upstream orientation, and travel speeds that optimize energy efficiency. The failure to minimize energy expenditures is sometimes due to environmental constraints that exceed the physiological capacities of migrants. Minimizing the probability of death due to exhaustion may be the major factor determining migratory behavior. Selection for energetic efficiency appears important only in cases where energy reserves are exhausted during migration.

Les chercheurs qui étudient le comportement migratoire chez les poissons acceptent de façon générale la minimisation des coûts énergétiques par unité de distance comme facteur d'optimalité régissant les migrations anadromes en rivière. Pour tester cette théorie, nous avons documenté à partir de la littérature les vitesses de déplacement et les dépenses énergétiques qui y sont associées pour 15 populations impliquant 9 espèces anadromes étudiées au cours de leur migration de reproduction. De plus, nous avons calculé une série de paramètres afin de décrire le comportement migratoire des poissons et l'hydrologie du système pour chaque population. Dans la majorité des cas, le coût par unité de distance n'est pas minimisé et la stratégie migratoire observée n'est pas conforme aux prédictions théoriques. Les populations qui effectuent une migration longue et difficile sont énergétiquement plus efficace que celles qui ont une migration courte. Seulement les populations qui utilisent toute leur énergie pour compléter la migration nagent à vitesse proche de la vitesse optimale théorique. Nous proposons que la longueur de la migration peut mener à une efficacité migratoire accrue en sélectionnant les migrateurs démontrant une plus grande taille, une meilleure précision dans l'orientation des mouvements et se déplaçant à vitesse proche de l'optimum. Plusieurs contraintes environnementales peuvent mener à une augmentation des coûts de migration chez certaines populations. La minimisation de la probabilité de mortalité causée par des vitesses de nage élevées pourrait être le facteur principal déterminant le comportement migratoire. Il semble que l'efficacité énergétique soit sélectionnée seulement dans les cas où les migrations sont très longues et mènent à l'épuisement des réserves énergétiques.

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The purpose of this paper is to test the hypothesis that anadromous fish behave so as to minimize energy costs per unit distance of migration. We document swimming speeds, travel speeds, and energy costs exhibited by 15 anadromous populations studied from the time of river entry to spawning. In cases where fish do not behave to minimize energy costs per unit distance, we consider the existence of environmental factors that limit the optimal strategy or factors other than energy conservation that determine migratory behavior.

Migration is important in the life cycles of many fish species

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and is typically considered an adaptation that increases fitness by enhancing growth, fecundity, and survival (Northcote 1978, 1984). It also involves important costs in time, energy, and risk that vary with distance migrated and the difficulties encountered during the trip. The final stages of the reproductive migration of anadromous species involve difficulties like crossing estuaries with tidally induced oscillations in current speed and direction, salinity, and temperature and facing unidirectional currents of up to 5–10 km·h⁻¹ near rapids and waterfalls. Anadromous species do not usually feed in freshwater, deriving the energy required for migration from reserves stored in muscles and viscera while at sea. In many cases, gonads ripen during migration, draining even more stored energy. Consequently, reproductive migrations may

lead to considerable loss of weight and energy which frequently causes high mortalities (Idler and Clemens 1959; Glebe and Leggett 1981b). Thus, one may expect costly migrations to act as strong selective agents for the evolution of traits that improve migratory success. The exceptionally high aerobic metabolic rate and swimming capacity of the sockeye salmon (*Oncorhynchus nerka*) (Brett 1964, 1965a, 1965b, 1967) are good examples of physiological traits appropriate for long and difficult migrations. Chum salmon (*Oncorhynchus keta*) (Beacham 1984) and pink salmon (*Oncorhynchus gorbuscha*) (Beacham 1985) spawning in large rivers have larger heads, fins, and caudal peduncles than do salmon from small rivers, suggesting that water flow velocity leads to morphological adaptations that improve migratory success. River harshness, as measured by the maximum distance that migrants penetrate into freshwater, is known to be correlated with differences in size, age at first reproduction, and date of river entry among populations of Atlantic salmon (*Salmo salar*) (Schaffer and Elson 1975).

One may also expect selection for behavioral traits that adjust time spent migrating and swimming speed to maximize fitness. The use of optimality theory, based on the hypothesis that natural selection tends to produce animals that are maximally efficient at doing all activities associated with propagating their genes (Davies and Krebs 1978), may serve as a general framework for the study of fish migratory behavior. Recently, Pyke (1981) reviewed the more likely optimality criteria for travel speeds and divided them into two main groups according to the purpose of movement. When travel is associated with foraging, animals can regulate their speed to maximize the net rate of energy gain, growth efficiency, or growth efficiency per unit ration (Ware 1975). When travel has nothing to do with foraging (e.g. reproductive migration), speed can be adjusted for minimizing predation (Peterson 1976), minimizing energy expenditure per unit distance (Weihs 1973a; Ware 1978), or minimizing energy expenditure per unit time (Tucker 1968). Any reduction in energy expenditure will permit an animal to accumulate a surplus of energy that may enhance fitness.

Students of fish migratory behavior generally believe that minimizing energetic cost per unit distance is the major criterion in the application of optimality theory to fish migratory behavior. This notion was established by Weihs (1973a) who developed a model, based on the hydrodynamics of swimming, which calculated that fish will minimize the cost of swimming per unit distance if they swim at speeds for which the energy requirement is about twice (1.7–2.3 times) that of the standard metabolic rate. This speed corresponds approximately to one body length per second ($1 \text{ Bl} \cdot \text{s}^{-1}$) but is highly variable depending on species, size, and physiological condition. Subsequently, other models describing the optimal travel strategy in terms of minimizing energy cost per unit distance have been developed (Weihs 1973b, 1973c, 1974; Ware 1978; Pyke 1981; Wakeman and Wohlschlag 1982). However, these models did not consider the importance of water currents, a dominant characteristic of many systems in which fish migrate. Weihs (1978) has shown theoretically that in areas where tides are directional, fish may achieve considerable energy savings by swimming in midwater at a constant speed relative to the bottom when the tide flows in the direction of migration and holding station on the sea floor when the tide flows in other directions. Such behavior, known as selective tidal stream transport, has been demonstrated in plaice

(*Pleuronectes platessa*) (Greer Walker et al. 1978) and can save up to 40% in energy cost compared with the alternative strategy of swimming continuously in the direction of overall movement (Weihs 1978). Trump and Leggett (1980) extended the analysis of migratory efficiency by eliminating Weihs's (1978) assumptions of constant current speed and constant swimming speed relative to the bottom. Their model predicts that the optimum swimming speed in a current is $U_0 + 1/b$ where U_0 is the residual or mean current and b is an empirical constant in the expression describing the relationship between swimming speed and oxygen consumption:

$$\log Y = \log C + bu$$

where Y = oxygen consumption (milligrams per kilogram per second), C = standard metabolic rate and u = swimming speed (body lengths per second). The constant b (seconds per body length) varies (according to species) between 0.2 and 0.5; a low value of b indicates an efficient swimmer and a high value indicates an inefficient swimmer (Priede 1985). Trump and Leggett's (1980) model also predicts that energy expenditure is minimized in variable tidal currents by swimming at a constant speed through the water even in cases where occasional retrograde motion over the bottom occurs. This type of behavior has been observed in sockeye salmon migrating in coastal water (Madison et al. 1972) and American shad (*Alosa sapidissima*) migrating in rivers (Leggett 1976).

Few studies of fish migratory behavior test the general hypothesis that anadromous fish behave so as to minimize energy cost per unit distance of migration. Although biotelemetry studies are numerous, the energetic efficiency of swimming behavior often cannot be evaluated because we lack detailed knowledge of speed and direction of the water currents experienced by migrating fish. In addition, biotelemetry studies rarely provide a description of swimming behavior over the total migration route (river's mouth to spawning grounds) because of the short time scales (hours and days) of most tracking studies. However, studies of the energy cost of migration based on observations of weight loss and lipid and protein metabolism, coupled with observations of migration length and duration, provide reliable estimates of energy cost per unit distance for a variety of species and hydrological conditions. When energetic cost per unit time of migration is known, average swimming speeds can be estimated from species-specific respirometry studies relating swimming speed to oxygen consumption. Thus, the combination of these studies can provide estimates of swimming speed (displacement per unit time through the water), travel speed (displacement per unit time over ground), and related energy costs.

Methods and Analysis

Data concerning migration energetics, swimming speed, and hydrology were available for 15 anadromous fish populations involving 9 species (Table 1). Evaluation of the total cost of migration based on the application of caloric equivalents to changes in protein and lipid content of gonads, viscera, and somatic tissues was available for the river lamprey (*Lampetra fluviatilis*) (Moore and Potter 1976), sea lamprey (*Petromyzon marinus*) (Beamish 1979, Beamish et al. 1979), alewife (*Alosa pseudoharengus*) (Parlee 1983), American shad (Glebe and Leggett 1981a, 1981b) Fraser River sockeye salmon (Idler and Clemens 1959), chum salmon (Pentagov et al. 1928),

TABLE 1. Characteristics of 15 anadromous fish runs obtained from the literature. Populations are presented in ascending order of body weight. Data sources are given in the text.

Species (No.)	Migration	Mean weight (g)	Mean length (cm)	Migration length		Relative estuary length	Vertical gradient (m·km ⁻¹)	Current speed (BL·s ⁻¹)	Water temperature (°C)	Total migration cost (kJ·kg ⁻¹)
				km	Body lengths					
River lamprey (<i>Lampetra fluviatilis</i>)	(1) Severn	55	30	100	3.3 × 10 ⁵	0.375	0.10	0.60	8	5109
Cisco (<i>Coregonus artedii</i>)	(2) Eastmain	310	29	33	1.1 × 10 ⁵	0.818	0.45	0.86	11	2114
Alewife (<i>Alosa pseudoharengus</i>)	(3) La Have	327	32	32	1.0 × 10 ⁵	—	—	—	—	884 ^a
Sea lamprey (<i>Petromyzon marinus</i>)	(4) St. John (N.B.)	896	77	140	1.8 × 10 ⁵	0.321	0.02	—	10	2280
American shad (<i>A. sapidissima</i>)	(5) St. Johns (Florida)	1 000	40	370	5.9 × 10 ⁵	0.135	0	—	21	6463
American shad	(6) York	1 300	45	80	1.86 × 10 ⁵	0.625	—	—	17	1520
American shad	(7) Connecticut	1 800	55	137	2.49 × 10 ⁵	0.310	0.22	1.00	16	2863
Sockeye salmon (<i>Oncorhynchus nerka</i>)	(8) Skeena	2 200	57	380	6.3 × 10 ⁵	0.131	1.84	3.33	13	3778
Sockeye salmon	(9) Fraser (Stuart lake run)	2 545	58	1152	1.74 × 10 ⁶	0.073	0.66	2.32	15	4555
Sockeye salmon	(10) Fraser (Chilko lake run)	2 545	58	596	1.0 × 10 ⁶	—	1.75	2.32	13	5070 ^a
Atlantic salmon (<i>Salmo salar</i>)	(11) Northwest Miramichi	2 900	74	113	1.5 × 10 ⁵	0.400	1.77	0.54	16	2032
Chum salmon (<i>O. keta</i>)	(12) Amur	3 900	64	1193	1.86 × 10 ⁶	0.084	0.25	1.26	12	6140
Atlantic salmon	(13) Spey	4 100	77	105	1.4 × 10 ⁵	0.020	—	—	—	1262
Chinook salmon (<i>O. tshawytscha</i>)	(14) Sacramento	10 000	86	1000	1.15 × 10 ⁶	0.100	1.00	—	—	3856
Chinook salmon	(15) Columbia	15 000	104	1134	1.10 × 10 ⁶	0.140	0.53	1.50	15	2852

^aEvaluation of the cost of migration does not include the estuary section.

chinook salmon (*Oncorhynchus tshawytscha*) (Greene 1926), River Spey Atlantic salmon (Paton 1898), and Eastmain River (James Bay) cisco (*Coregonus artedii*) (Lambert and J. J. Dodson, in prep.). Indirect evaluation of the cost of migration was obtained for Skeena River sockeye salmon (Brett 1983) and was calculated from weight loss measurements during migration for Miramichi River Atlantic salmon (Belding 1934). Changes in tissue mass parallel changes in tissue energy content (Glebe and Leggett 1981b) and thus serve as estimates of energy use during migration. The cost of migration was evaluated as:

$$Mc = x(a - b) - y(c - d)$$

where Mc = absolute cost of migration (kilojoules), a = net dry weight (total dry weight less gonads) of fish prior to upstream migration (grams), b = net dry weight of fish prior to spawning (grams), c = dry weight of gonads prior to spawning (grams), and d = dry weight of gonads prior to upstream migration (grams). Dry weight was calculated by subtracting moisture content values obtained by Paton (1898) for Atlantic salmon. Protein catabolism accounted for about 20% of the energy liberated during the reproductive migration of River Spey Atlantic salmon (Paton 1898). We assumed a similar situation for Miramichi River Atlantic salmon and calculated that 71% of their dry weight loss was due to lipid depletion and 29% due to protein depletion. Using the energetic equivalents of protein ($23.85 \text{ kJ}\cdot\text{g}^{-1}$) and lipid ($38.91 \text{ kJ}\cdot\text{g}^{-1}$), we calculated an energetic equivalent, $x = 34.54 \text{ kJ}\cdot\text{g}^{-1}$, to convert dry weight to energy loss. A conversion factor, $y = 25.52 \text{ kJ}\cdot\text{g}^{-1}$, was applied to gonad weight, as it represents energy content of gonads of four species (range $24.69\text{--}25.94 \text{ kJ}\cdot\text{g}^{-1}$; Saldama and Venables 1983).

Five environmental variables were used to characterize the freshwater reproductive migration of each population. The first variable considered was the length of the migration measured from the river's mouth to the spawning grounds. Migration length does not include the estuary in the case of the alewife and Chilko sockeye salmon. Migration length in the case of Stuart sockeye is overestimated, as it includes 58 km of coastal migration. Migration length was divided by mean body length in each case to produce an estimate of relative migration length in order to render the values comparable among migrants of different size. The second variable considered was estuary length measured from the river's mouth to the head of the tide. In each case, this value was divided by total migration length to provide an estimate of the proportion of the migration influenced by reversing tidal currents (relative estuary length). Other variables considered were the mean vertical gradient (metres per kilometre) estimated from topographical maps, mean water temperature during the migration, and mean current speed in the river. Mean current speed was divided by mean body length in each case to render current speed data comparable among populations. Current speed data were obtained from the above studies in the case of sockeye and chum salmon populations, from Dodson et al. (1985) for Eastmain River cisco, from Osborne (1961) for Columbia River Chinook salmon, from Stasko et al. (1973) for Miramichi River Atlantic salmon, and from Leggett (1976) for American shad. Water temperature data were obtained from the above studies except in the case of Atlantic salmon (Banks 1969) and American shad (Leggett and Whitney 1972).

Parameter Calculations

The total cost of the reproductive migration for each population was calculated for a female of mean weight for the population. Males were not considered because data were often incomplete. The cost of migration per unit distance (kilojoules per kilometre) or unit time (kilojoules per day) was calculated by dividing total cost by migration length and duration. All estimates are expressed per unit body weight (kilograms) to render the data comparable.

Most published telemetry studies do not provide accurate measures of swimming speed relative to the water because they have not adequately documented current speed and direction experienced by the fish. However, the cost of migration per unit time is a direct consequence of the mean swimming activity of fasting fish. Thus, cost per unit time data permit an estimation of mean swimming speed relative to the water from regressions relating energy expenditure with swimming speed that are empirically determined using respirometry techniques. For example, Brett (1965a) used this method to demonstrate that Fraser River sockeye salmon that expend $177 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$ (Idler and Clemens 1959) were swimming on average at $1.33 \text{ m}\cdot\text{s}^{-1}$. Mean swimming speed for sockeye, chinook, chum, and Atlantic salmon were predicted using the relationship between energy expenditure per unit time and swimming speed elaborated by Brett and Glass (1973). Results obtained by Bernatchez and Dodson (1985) were used for cisco and American shad and results reported by Beamish (1973) and Claridge and Potter (1975) were used for sea lamprey and river lamprey, respectively.

Mean rate of displacement (kilometres per day) was calculated by dividing migration length by the time from the start of the migration to the spawning period. Observed rates of displacement were noted in some cases, and such values are comparable with our calculated rates. For example, Leggett (1976) observed a mean displacement rate of $6 \text{ km}\cdot\text{d}^{-1}$ for American shad migrating up the Connecticut River based on telemetry techniques. The mean time from river entry to spawning is 22 d, and the distance covered 137 km for a comparable calculated value of $6.2 \text{ km}\cdot\text{d}^{-1}$.

Directionality of movement is an important component of migratory behavior. However, quantitative estimates of orientation could not be obtained from telemetry studies, as the typically short observation periods preclude meaningful measurements of directionality, and such studies have not been conducted on all species. Thus, we calculated an index of directionality by dividing the mean rate of displacement by the mean swimming speed relative to the water. The maximum value of the index is 1 and corresponds to an ideal situation where all swimming activity is translated into upstream displacement and, thus, movement is perfectly oriented upstream. Values less than 1 imply either meandering (low directionality, holding position) or the effects of currents; that is, the greater the current velocity the fish must swim against, the greater the swimming activity necessary to cover a unit distance over ground. Although currents surely affect the swimming activity of fish, current speed was not correlated with the directionality index (Spearman's correlation; $r = 0.185$, $p = 0.59$). Thus, we propose that decreasing values of directionality index probably reflect greater meandering behavior and that the index represents a comparative estimate of the directionality and persistence of upstream migration among populations.

To provide a comparative measure of the energetic effi-

TABLE 2. Characteristics of anadromous fish runs calculated from data presented in Table 1.

Species (No.)	Cost per unit distance (kJ·kg ⁻¹ ·km ⁻¹)	Cost per unit time (kJ·kg ⁻¹ ·d ⁻¹)	Mean swimming speed (BL·s ⁻¹)	Mean displacement rate		Directionality index (no units)	Optimal displacement rate (BL·s ⁻¹)	Optimal displacement index (no units)
				km·d ⁻¹	BL·s ⁻¹			
River lamprey (1)	51.09	34.1	0.33	0.6	0.023	0.070	0.77	0.030
Cisco (2)	64.06	37.8	0.86	0.6	0.023	0.026	1.16	0.019
Alewife (3)	27.62	—	—	5.4	0.195	—	0.80	0.244
Sea lamprey (4)	16.29	27.9	0.13	1.8	0.027	0.207	0.33	0.082
American shad (5)	17.47	155.1	1.50	8.8	0.254	0.169	0.70	0.363
American shad (6)	19.00	101.0	1.00	4.6	0.118	0.118	0.65	0.182
American shad (7)	20.89	130.1	1.09	6.0	0.126	0.116	0.60	0.210
Sockeye salmon (8)	9.94	179.9	2.77	18.0	0.365	0.132	1.03	0.354
Sockeye salmon (9)	3.95	168.7	2.71	42.6	0.850	0.314	1.03	0.825
Sockeye salmon (10)	8.51	117.8	2.25	13.9	0.275	0.122	1.03	0.267
Atlantic salmon (11)	17.98	16.3	0.10	0.9	0.014	0.140	0.90	0.016
Chum salmon (12)	5.15	198.1	2.43	45.0	0.814	0.334	1.09	0.747
Atlantic salmon (13)	12.02	—	—	—	—	—	—	—
Chinook salmon (14)	3.86	27.6	0.67	7.1	0.096	0.143	1.10	0.087
Chinook salmon (15)	2.52	66.3	1.40	26.0	0.289	0.207	0.89	0.325

TABLE 3. Spearman correlation matrix. (**p*(*r*) < 0.05; ***p*(*r*) < 0.01; ****p*(*r*) < 0.001).

	Cost·distance ⁻¹	Weight	Optimal displacement index	Migration length	Directionality	Relative estuary length	Cost·time ⁻¹	Current speed	Vertical gradient
Weight	-0.836***								
Optimal displacement index	-0.569*	0.365							
Migration length	-0.779***	0.527*	0.684**						
Directionality	-0.787***	0.576*	0.608*	0.630*					
Relative estuary length	0.736**	-0.615*	-0.811***	-0.577*	-0.722**				
Cost·time ⁻¹	-0.209	0.085	0.879***	0.533	0.283	-0.552			
Current speed	-0.644*	0.723**	0.470	0.671*	0.185	-0.571	0.452		
Vertical gradient	-0.350	0.539	-0.021	0.201	-0.088	-0.209	-0.035	0.713*	
Total cost	-0.336	0.045	0.516	0.771***	0.305	-0.352	0.505	0.247	-0.308

ciency of displacement rate, an index of optimal displacement was calculated for each population. The index was calculated by dividing observed displacement rate by a calculated optimal displacement rate. This latter calculation was based on Trump and Leggett's (1980) prediction that optimal displacement rate is independent of current speed and should always equal 1/*b*, the theoretical ground speed at which energy cost per unit distance is minimized. Theoretical predictions of this speed were not made in our study. Rather, the empirical least costly ground speed was calculated for each species using the relationships between energy expenditure and swimming speed reported in the respirometry studies cited previously. Our calculated optimal ground speeds (mean of 0.88 BL·S⁻¹) fall within the range of Trump and Leggett's theoretical predictions (0.6–2.0 BL·S⁻¹). An optimal displacement index value of 1 corresponds to the situation where observed ground speed (displacement rate) minimizes energy cost per unit distance. Index values less than 1 indicate ground speeds that are below optimal, whereas values greater than 1 indicate ground speeds in excess of the optimal displacement rate.

A Spearman correlation matrix was generated to analyse the relationship between the above variables. The null hypothesis that the variables were not correlated was rejected at *p* = 0.05.

Results

Anadromous freshwater migrations are very different in terms of the body size of migrating fish, the type of river, and the distance traversed (Table 1). The total cost of migration is important in each case but varies only by a factor of 5 (1262–6463 kJ·kg⁻¹) as compared with the length of the migration which varies by a factor of 36(33–1193 km).

Anadromous migrants do not exhibit a general pattern of migratory performance (Table 2). In some cases, migration can be very slow, involving much meandering and low swimming speed (e.g. river lamprey), or very fast, well oriented and requiring high levels of activity throughout the migration (e.g. Fraser River sockeye salmon and Amur River chum salmon). An important observation is that mean displacement rate never exceeds the optimum displacement rate and is approached only by Stuart Lake sockeye salmon and by chum salmon. Except for these two cases, the rates of displacement represent less than 40% of the optimum.

Increasing energy efficiency of migration is associated with distance traveled, as demonstrated by the strong negative correlation between the cost of migration per unit distance and migration length (Table 3). This relationship is described by an

exponential function (Fig. 1a). Cost per unit distance also decreases exponentially with increasing body weight (Fig. 1b) and as ground speed approaches the optimum (Fig. 1c). Meandering behavior also leads to poor energy efficiency, as illustrated by the strong negative relationship between cost per unit distance and the directionality index (Fig. 1d). Body weight, optimal displacement index, and directionality index are all correlated with migration length (Table 3). In addition, populations that must traverse relatively short estuaries exhibit less overall meandering and travel at speeds closer to the optimum than do fishes that traverse relatively long estuaries (Table 3).

This analysis does not permit us to define the relative contribution of each variable to migratory efficiency because of correlations among variables. The limited number of observations prevents the application of appropriate statistical procedures to quantify the influence of such partially correlated variables. Thus, although the following discussion deals with each statistical relationship as a separate hypothesis, the complex of interrelationships among variables remains to be defined.

Discussion

Energetic Efficiency of Migration

The difference in migratory efficiency among populations is illustrated by the range of energy costs per unit distance ($2.52\text{--}64.06 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$). The theoretical minimum costs of transport per unit distance, based on Trump and Leggett's (1980) prediction that optimal swimming speeds equals $U_0 + 1/b$ and calculated for those migrations where mean current velocity was available (nine cases, Table 1), vary from $1.10 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$ for Columbia River chinook salmon to $5.88 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$ for river lamprey. Thus, it appears that in cases such as the Stuart Lake stock of sockeye and the chum and chinook salmon analysed, migratory efficiency is close to the theoretical optimum. In most cases, however, cost per unit distance is not minimized and observed migratory efficiency is far from the theoretical optimum.

The observation that energetic efficiency of migration increases with the length of migration (Fig. 1a) is consistent with an evolutionary interpretation of variability in migratory efficiency. Migratory efficiency is a function of the selective pressure imposed by the difficulty of a migration if we assume that the distance to the spawning ground is a major factor contributing to the difficulty of migration (Schaffer and Elson 1975). Our results demonstrate that anadromous populations that make long or difficult migrations are more efficient in their use of energy reserves than populations that make shorter migrations. We propose that the difficulty of migration selects for efficient migrators that are larger, orient more accurately, and travel at speeds that approach the theoretical optimum in terms of energy efficiency.

It has been demonstrated experimentally that larger body size increases metabolic efficiency in terms of energy expended per unit body weight and swimming capacity (reviewed by Beamish 1978). Several authors have provided evidence that the length of migration may have selected for increased body size in Atlantic salmon (Schaffer and Elson 1975) and American shad (Glebe and Leggett 1981b). The results of our survey suggest that previous findings indicating that migration length selects for increased body size and hence greater energetic efficiency may be generalized among anadromous fish populations.

A second factor contributing to migratory cost in the precision and persistence of upstream orientation, with increased meandering leading to increased cost per unit distance. The negative relationship between directionality index and the relative length of the estuary suggests that traversing estuaries contributes significantly to meandering. This phenomenon is illustrated by telemetry studies conducted in estuarine and coastal environments. Much meandering behavior alternating with periods of holding position and retrograde motion is characteristic of American shad (Dodson et al. 1972), Atlantic salmon (Stasko 1975; Brawn 1982), sockeye salmon (Groot et al. 1975), and cisco (Dodson et al. 1985). This behavior is due in part to the physiological stress of passing from saltwater to freshwater. However, such behavior is also associated with problems of orientation. Unidirectional currents encountered above the head of the tide provide strong directional cues and stimulate upstream movement directly by water flowing over the body or by visual, tactile, and olfactory stimuli (Arnold 1974). However, tidally induced oscillations in current direction encountered in estuaries demand tide-specific rheotactic behavior (Dodson and Dohse 1984) or some other mechanism of orientation independent of currents if fish are to avoid swimming back and forth over the same ground. How fish achieve this and the relative precision of the mechanisms of orientation involved remain questions of major interest to students of fish migration (Arnold 1981).

As displacement rate approaches the theoretical optimum, important energy savings can be achieved (Fig. 1c). However, only the Pacific salmon populations surveyed in our study approach this optimal state. Pacific salmon spawn only once in their life and despite their outstanding migratory efficiency, they usually terminate their reproductive migration with metabolic fuel reserves nearly exhausted. Thus, fuel economy is essential for successful reproduction. Iteroparous species such as American shad (Connecticut and York rivers), cisco, Atlantic salmon, and alewife could also benefit from minimizing costs to improve the probability of successfully returning to sea and surviving for future spawnings. This, however, does not appear to be a strong selective factor. Optimal displacement rates that minimize energy expenditure per unit distance are achieved only in cases where migration length leads to extreme energy expenditure.

The Problem of Environmental Constraints

The failure to minimize energy expenditure per unit distance is in many cases due to the presence of environmental constraints that exceed the physiological capacities of migrants. For example, in situations of high current speeds, theoretically optimal ground speeds may be higher than maximum sustainable swimming speeds, resulting in fatigue and long periods of inactivity that permit recuperation. Periods of active swimming followed by periods of holding position during migration in rivers have been documented for several anadromous populations (e.g. Ellis 1966; Leggett 1976; Power and McCleave 1980) although it is not clear whether such behavior is due to fatigue. In some species where swimming capacity has been experimentally evaluated (sockeye salmon, Brett and Glass 1973; cisco, Bernatchez and Dodson 1985), it is clear that current speeds encountered in some parts of the migration must lead to exhaustion.

Some anadromous populations face environmental constraints that force them to spend long periods in rivers without feeding, thus augmenting the cost per unit distance of the

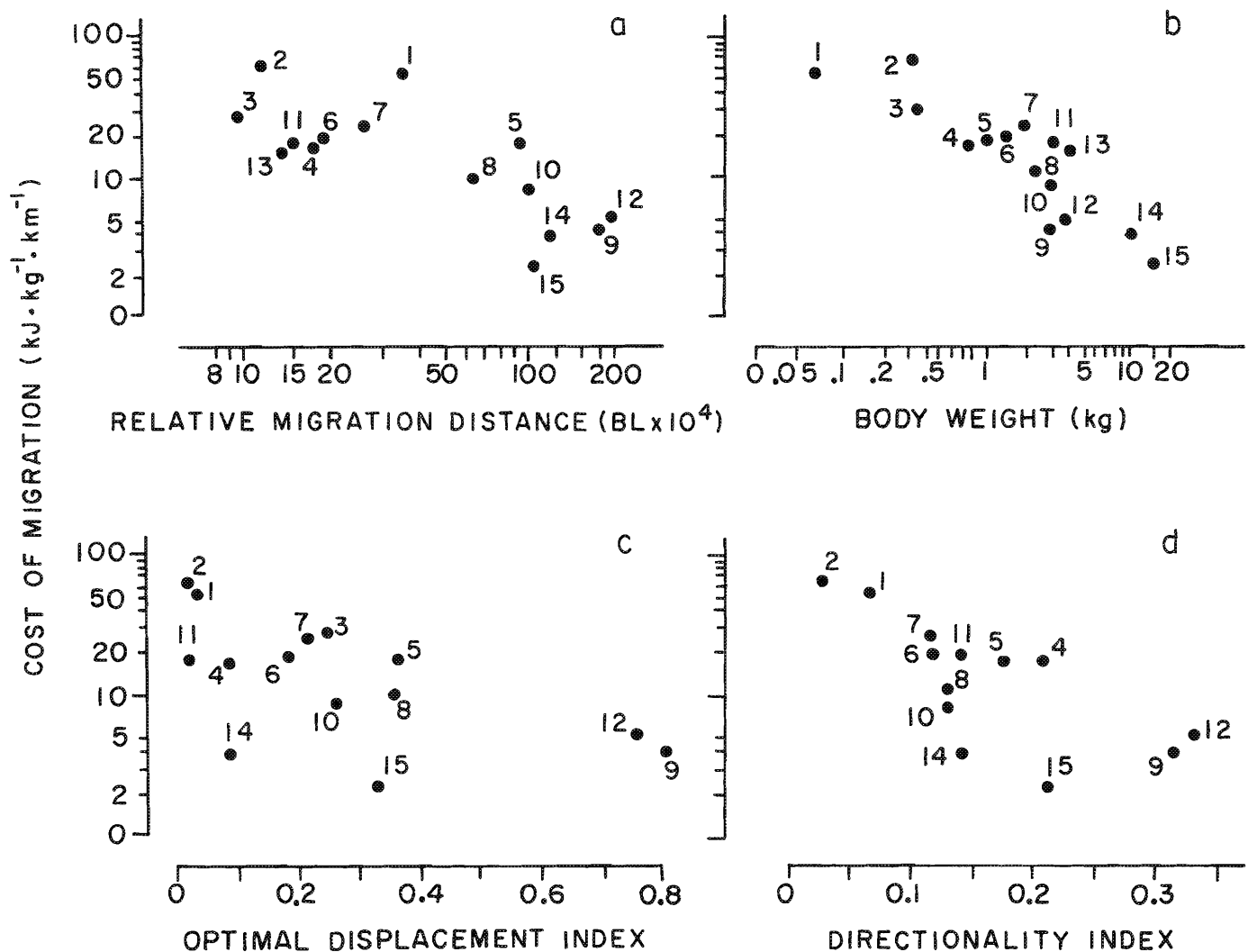


FIG. 1. Relationship between the energetic cost of migration (logarithmic scale) and (a) relative migration distance (logarithmic scale), (b) body weight (logarithmic scale), (c) optimal displacement index (arithmetic scale), and (d) directionality index (arithmetic scale). Numbers refer to anadromous populations identified in Table 1.

freshwater migration. Such situations are particularly evident in northern rivers. Low water temperatures lead to poor swimming capacity by diminishing oxygen uptake and the metabolic scope for activity (e.g. Bernatchez and Dodson 1985) and place a ceiling on the maximum swimming speed attainable by fish (Wardle 1981). We have proposed that such constraints may require cisco to traverse rapids downstream of spawning grounds 6–8 wk before spawning when water temperatures are relatively high (12°C) compared with temperatures at which these fish spawn (<5°C) (Dodson et al. 1985; Bernatchez and Dodson 1985). In the case of Atlantic salmon homing to rivers of Ungava Bay, northern Quebec, Power (1981) hypothesized that sea and river temperatures confine their migrations to a very short period. Adult salmon arrive in the estuaries of their spawning rivers in midsummer as suitable temperatures are attained in Ungava Bay (> 3°C). About 85% of the males have immature gonads when they arrive; they must remain in freshwater over 12 mo before their gonads ripen due to the short period of time during which river temperatures are suitable for maturation. Such protracted periods of freshwater residence, related mainly to temperature constraints, are not unusual among northern anadromous salmonid populations. Arctic

char (*Salvelinus alpinus*), studied in the Northwest Territories of Canada, pass 1 yr in freshwater prior to spawning (Dutil 1982).

Power Budgeting vs. Energy Saving

We have until now considered migratory performance only in terms of minimizing energy expenditures per unit distance. However, other biological variables may be more important than energy savings in influencing migratory behavior. A fish working at moderate power outputs may be assumed to have a small probability of mortality, but as metabolic rate approaches the upper limits of metabolic scope, the probability of death due to exhaustion and failure of homeostasis also increases (Priede 1977). Power budgeting refers to the immediate energetic objective of regulating metabolism on a minute-by-minute basis so as to remain within the limits of metabolic scope (Priede 1985). Priede argued that power budgeting may be more important than energy saved in the long-term energy budget. Animals avoid working at high metabolic rates to minimize the probability of mortality; fitness is increased because of increased probability of survival to reproductive age (Priede 1985). Applying this idea to anadromous reproduc-

tive migrations, fish may behave so as to minimize the proportion of time spent at exhausting activity levels to maximize the probability of survival during the migration. However, they must store sufficient energy reserves to afford the increased costs that such behavior may involve. Only in cases of extremely difficult migrations during which all available energy reserves are exhausted does selection for energetic efficiency appear to become important.

The basic assumption that migratory behaviors can be viewed as adaptations for minimizing energy costs is not only inappropriate in many cases but has unduly influenced the way in which we characterize anadromous migrations. Most theoretical treatments emphasize the energetic consequences of different swimming strategies but neglect the precision of upstream orientation. This bias may lead to erroneous interpretations of different swimming strategies. For example, Glebe and Leggett (1981b) predicted that cost per unit distance, based on swimming speed observations, is higher for semelparous than for iteroparous species and concluded that semelparous species swim at speeds close to maximum sustainable whereas iteroparous species swim close to optimum speeds, thereby minimizing the energy costs of migration and improving the probability of return to sea. However, calculations of energy cost per unit distance and optimal displacement index (Table 2) reveal that semelparous sockeye salmon are more energy efficient than iteroparous American shad (Connecticut River stock) in spite of differences in their mean swimming speeds. This difference in overall energetic efficiency can be explained in part by the meandering nature of the shad migration compared with that of sockeye salmon. The fact that precise orientation is not a part of the behavioral repertoire of many migratory fish (Leggett 1984) lends support to the hypothesis that energy efficiency is not the main factor being optimized in most anadromous migrations. The high energetic efficiency and apparently precise upstream orientation of some stocks of Pacific salmon (Table 2) are exceptional and appear to be the result of the selective pressure imposed by the length of migration.

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