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Estimating the energetic cost of abiotic conditions using foraging behaviour

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ABSTRACT

Questions: What are the energetic costs associated with different temperatures and salinities? How do these costs change as a result of physiological development and how do they affect habitat choice?

Organism: Juvenile chinook salmon, *Oncorhynchus tshawytscha*.

Methods: We quantified energetic costs by estimating the quitting harvest rate of juvenile salmon expressing different amounts of osmoregulatory enzyme activity (i.e. different stages of smolting) in habitats that differed in either temperature or salinity.

Results: The cost for saltwater-preferring fish to forage in freshwater was 1.65 times greater than the cost for freshwater-preferring fish to forage in saltwater. The cost of foraging in freshwater was positively correlated with osmoregulatory enzyme activity among saltwater-preferring fish but, surprisingly, the cost of foraging in saltwater was not correlated with enzyme activity among freshwater-preferring fish. Salmon had no preference for water of 8.6°C over that of 12.6°C, but did prefer water of 8.9°C over that of 15.7°C. The costs associated with foraging in cooler or warmer water were equal when habitats differed by only 4°C, but when habitats differed by 7°C the cost of foraging in warmer water was 1.72 times greater than the cost of foraging in cooler water. For the range of conditions considered here, the cost of foraging in different salinities versus different temperatures is very similar.

Conclusion: Foraging behaviour can be used to estimate the energetic costs paid by animals exposed to different abiotic conditions and how these costs are influenced by changes in their physiological state.

Keywords: giving-up density, habitat choice, Na^+/K^+-ATPase, salinity, temperature.

INTRODUCTION

To predict habitat choice, it is necessary to determine which habitat provides the maximal difference between energetic gains and costs (Stephens and Krebs, 1986). Metabolic costs are relatively straightforward to measure and may vary depending on the state of the animal, such as its body size (Elliott, 1976) or developmental stage (Rowe and Ludwig, 1991; Morgan and

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Iwama, 1998). Costs that are more difficult to measure include those associated with biotic factors, such as predation risk (Lima and Dill, 1990) or intraspecific competition (Sutherland *et al.*, 1988; Grand and Dill, 1997), and abiotic factors that alter metabolic requirements, such as temperature (Crowder and Magnuson, 1983; Wildhaber and Crowder, 1991; Hilton *et al.*, 1999) or salinity (McGaw, 2001). When all these costs vary simultaneously, predicting habitat choice can be difficult.

When juvenile Pacific salmon (*Oncorhynchus* spp.) migrate from freshwater natal streams through estuaries to feeding areas in the ocean, they are confronted with complex and dynamic patterns of spatial and temporal variation in abiotic factors, particularly water salinity and temperature. Energetic costs associated with changes in salinity are influenced by the salmon's developmental stage (Morgan and Iwama, 1991). When salmon hatch they are hyper-osmotic to their environment and must maintain homeostasis by excreting excess water via their kidneys. As salmon develop from the freshwater parr stage into smolts, they experience a series of physiological, morphological, and behavioural changes that increase saltwater tolerance (McCormick and Saunders, 1987; Boeuf, 1993). One prominent physiological change is an increase in gill Na^+/K^+-ATPase, an enzyme that enables fish to eliminate excess salt through active ion transport (Zaugg and McLain, 1970; Saunders and Henderson, 1978; McCormick and Saunders, 1987). As a result of these physiological changes, smolts should be more efficient at maintaining osmotic balance in saltwater than parr, which should be more efficient in freshwater (Fig. 1).

Energetic costs are also dependent on water temperature. Fish in warmer habitats have higher metabolic rates and, therefore, higher energetic costs than fish in cooler habitats. When resources are insufficient to meet metabolic demands, fish move to cooler water where their metabolic costs are reduced (Elliott, 1982). However, if resources are abundant, warmer habitats should be preferred because the rate at which an individual can process food is increased, resulting in increased growth rate (Brett and Higgs, 1970; Elliott, 1982). The fish's state, specifically body size, is also an important predictor of temperature preference. Larger fish need a greater net energetic intake to survive in warm water than smaller fish; therefore, as food availability decreases, larger fish should move to cooler water at a higher food density than smaller fish (Hughes and Grand, 2000). Consequently, a fish's temperature preference should be dependent on both food availability and body size.

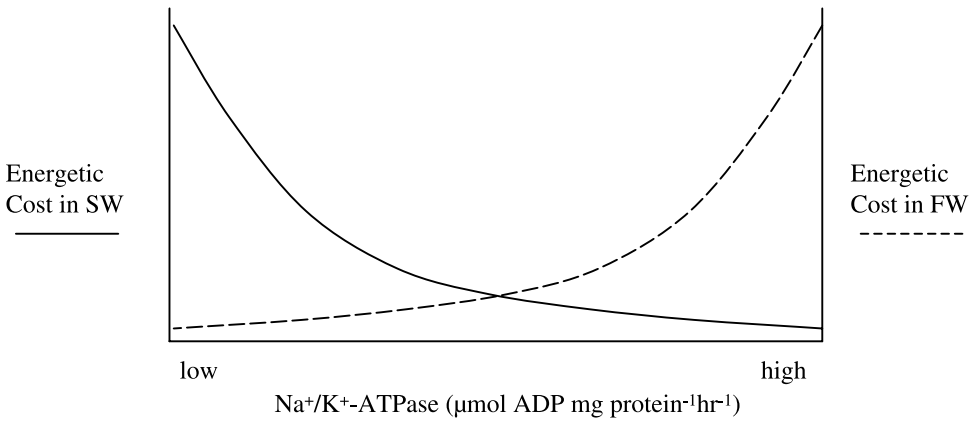


Fig. 1. Illustration of how energetic costs in freshwater (FW) or saltwater (SW) habitats are predicted to change as a function of gill Na^+/K^+-ATPase activity, a measure of developmental stage.

To predict habitat choice of salmonids, energetic costs must be quantified. Estimates of the metabolic costs paid by salmon in habitats of different salinities and temperatures are common in the literature (e.g. Rao, 1967; Morgan and Iwama, 1991, 1998; Kirschner, 1993; Kieffer *et al.*, 1998; Morgan and Metcalfe, 2001). However, the habitat with the lowest metabolic cost may not be preferred if biotic costs are too high, reducing the fish's net energetic gain. Consequently, predicting habitat choice requires quantification of the total energetic cost of different habitats, as well as the benefits to be obtained there.

The total cost of a habitat can be quantified using behavioural titration. Behavioural titration is based on the assumption that animals behave to maximize their net energetic gain. Consequently, an animal should choose a habitat as long as the net energetic gain of foraging there exceeds the net energetic gain of foraging in an alternate habitat (Kotler and Blaustein, 1995). There are two commonly used behavioural titration approaches for quantifying cost differences between two habitats: the giving-up density approach, which assumes that cost can be quantified based on the density of food remaining in a habitat when an animal leaves for an alternate, less costly, one (e.g. Brown, 1988; Kotler and Blaustein, 1995; Kilpatrick, 2003; Alofs and Polivka, 2004; Brown and Kotler, 2004), and the ideal free distribution approach, which assumes that the cost can be quantified based on how animals distribute themselves between habitats (e.g. Fretwell and Lucas, 1970; Abrahams and Dill, 1989; Grand, 1997; Nonacs and Dill, 1990; Abramsky *et al.*, 2000). Studies based on the ideal free distribution have demonstrated that the amount of food necessary to offset the increased cost of one habitat relative to another can be calculated, and that the redistribution of food according to this calculation will cause fish to redistribute themselves equally between habitats (Abrahams and Dill, 1989; Grand and Dill, 1997; Webster and Dill, 2006). The predictable response of the fish to changes in food availability provides strong support for the assumption, implicit in all behavioural titrations, that fish assess, and respond to, changes in the net energetic value of habitats.

In this study, we used behavioural titration to quantify the cost paid by salmon in habitats that differed in salinity and temperature by examining the patch-leaving decisions of juvenile chinook salmon (*Oncorhynchus tshawytscha*) under different salinity and temperature conditions, and by examining how these decisions change as a result of changes in the animal's physiological state. We expected (i) that when food was not sufficiently abundant to meet the energetic demands of a warm water habitat, fish would prefer cooler water, and (ii) that the energetic cost of using habitats that differed in salinity should vary depending on the osmoregulatory ability of fish.

METHODS

We used behavioural titration to quantify the energetic costs associated with different salinities and temperatures. Behavioural titration is based on the idea that when an animal's rate of energy gain in a habitat falls below its costs, it should stop foraging and seek another habitat (Brown, 1988). The animal's intake rate at the time it leaves the original habitat is referred to as the 'quitting harvest rate' (Pyke, 1978, 1980; Hodges, 1981). The difference in the quitting harvest rates associated with two different environmental conditions is a measure of the difference in the cost of residing in them. Most studies that are based on the quitting harvest rate approach assume that a forager's intake rate is dependent only on prey density and, therefore, that the amount of food remaining in the habitat when the animal leaves (referred to as the giving-up density) can be used as a surrogate for quitting harvest rate (Brown, 1988, 1992). However, if the animal's intake rate is altered by experimental conditions,

the cost estimates derived from a study based on giving-up density would be incorrect (Price and Correll, 2001). To prevent this possibility, we measured quitting harvest rate rather than giving-up density.

To quantify the energetic costs associated with different salinities and temperatures, we conducted two sets of experiments in which salmon were given choices between habitats that differed in either salinity or temperature. In the absence of food, we assumed that the fish would prefer the habitat that offered the lowest energetic cost (Fig. 2A). Food was then added to the habitat that was not preferred by the fish (hereafter referred to as the alternate habitat) to make its net benefit greater than that of the preferred habitat (Fig. 2B). As the food is consumed in the alternate habitat, the net energetic intake rate is reduced. The fish should return to the initially preferred habitat when the net energetic intake rate in the alternate habitat decreases to a point where it is just below the costs in the preferred habitat; the intake rate at this point is referred to as the quitting harvest rate (Fig. 2C). Individual variation that affects the energetic costs of the two habitats, such as a change in an individual's state, will result in a shift in the quitting harvest rate. A decrease in energetic cost in the more costly habitat will result in a decrease in the quitting harvest rate; conversely, an increase in energetic cost in the more costly habitat will result in an increase in the quitting harvest rate.

Fish and experimental set-up

The experiments were conducted on hatchery reared, young-of-the-year, ocean-type chinook salmon (*O. tshawytscha*) from the Chilliwack River (Chilliwack, BC) brood stock. The early life history of this stock of chinook involves smolting and migrating to the estuary in early May, spending days to months in the estuary, depending on conditions, and then continuing on to the ocean. Fish were collected from Chilliwack hatchery in March 2004 (fish were approximately 90 days old) and kept in an outdoor 2000-litre flow-through tank maintained under natural photoperiod and continuously supplied with air-equilibrated well water (salinity 0‰, temperature 11.4 ± 0.1°C, dissolved oxygen 95.3 ± 1.3% air saturation; mean ± standard deviation). Fish were fed a ration (2% of biomass per day) of commercial salmon pellets (EWOS Canada Ltd.) twice daily. Experiments were conducted between 18 April and 20 May (salinity trials) and between 2 June and 2 July (temperature trials).

The experiments were conducted in 20-litre aquaria ($41 \times 20 \times 25$ cm) divided into two habitats by 10-cm high clear Plexiglas™ dividers. The two habitats were kept at either different temperatures or different salinities using a duplex flow-through system. A 'bridge' of water across the divider was formed by creating a layer of fresh or warm water over the denser salt or cold water (Fig. 3), thus allowing the fish freedom to move between the two habitats at any time. Aquaria were maintained under a 16 : 8 day/night cycle.

Experimental procedures

The study consisted of three experiments each involving an acclimation phase. The first experiment characterized the intake rate curve to test the assumption of quitting harvest rate theory that fish experience a steadily diminishing intake rate in the apparatus. The second experiment quantified the difference in energetic cost associated with residency in habitats of different salinity. The third experiment quantified the difference in energetic cost associated with residency in habitats of different temperature.

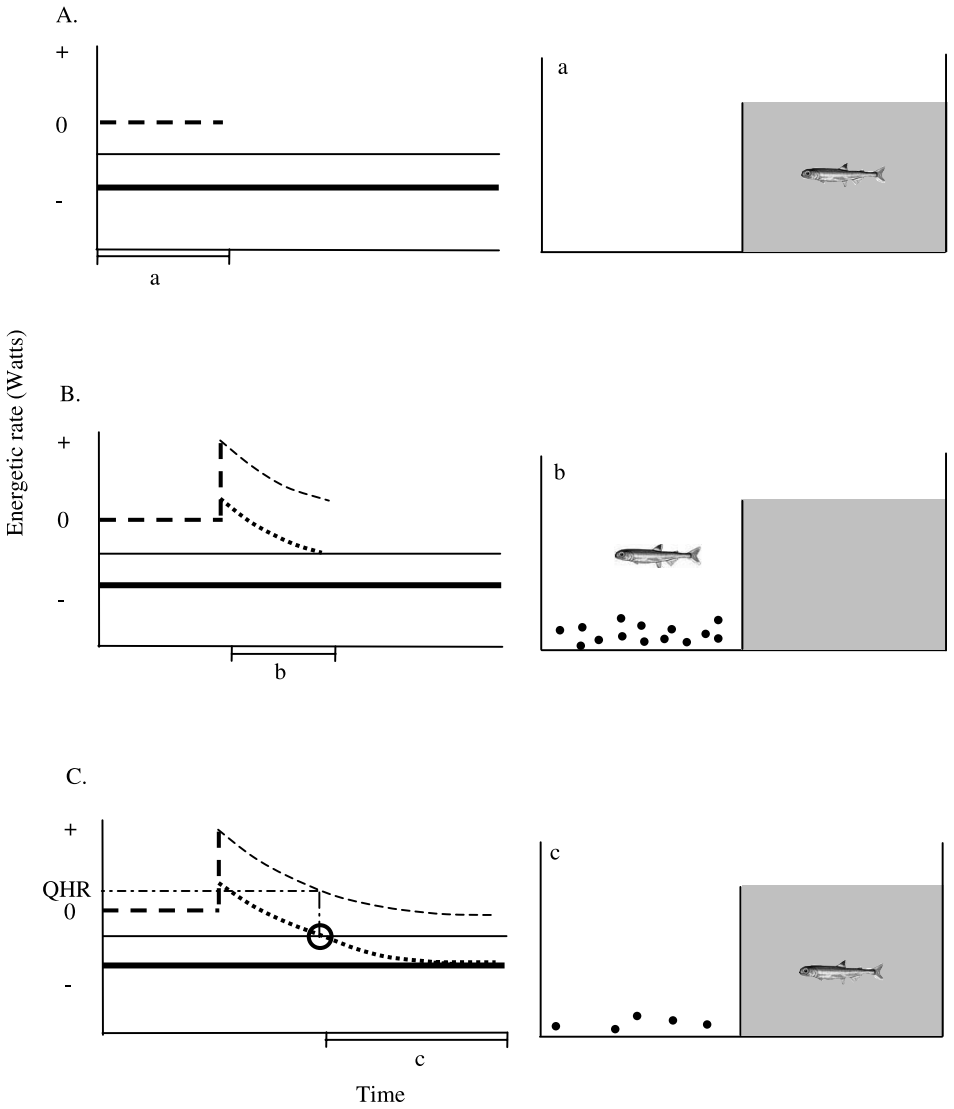


Fig. 2. Schematic description of when and why a forager should switch between two habitats that differ in their costs and intake rates. Energetic cost in habitat B (in this case the saltwater habitat; thin solid line) is lower (less negative) than in habitat A (in this case the freshwater habitat; thick solid line). (a) In the absence of food in habitats A and B, the forager will prefer habitat B. (b) If a depletable food source is added to habitat A (dashed line), the forager will prefer habitat A as long as the net gain (dotted line: gain in habitat A minus the cost in habitat A) is greater than costs in habitat B. (c) When the food is depleted to the point at which the forager's net gain in habitat A falls below costs in habitat B (○), the forager will return to habitat B. The harvest rate at this point is referred to as the quitting harvest rate (QHR).

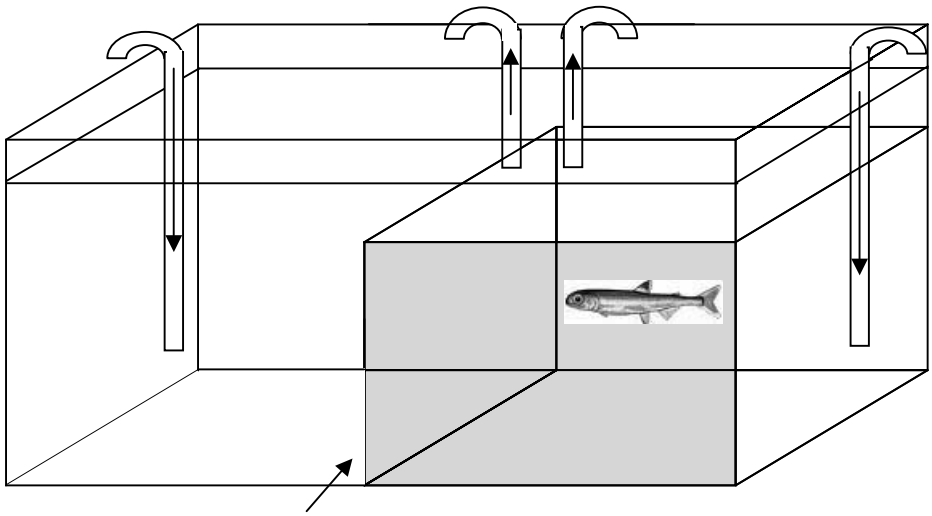


Fig. 3. Apparatus used during the experimental trials. Habitats A and B are separated by a clear Plexiglas™ divider and differ in either salinity or temperature. The less dense water in habitat A (freshwater in salinity experiments and cold water in temperature experiments) overflowed the central barrier, forming a fresh- or cold-water bridge that the fish could use to move between habitats. Temperature, salinity, and oxygen concentrations were maintained using a duplex flow-through system (arrows indicate water flow) that replaced the water on either side of the apparatus.

Acclimation

Fish were acclimated to the experimental set-up and a new food type for 12 days. During this time, groups of eight fish were placed in 60-litre aquaria that were set up the same way as the experimental tanks, but the two habitats were identical. The aquaria were continuously supplied with well water (temperature 11.4 ± 0.1°C). Fish were fed capelin (*Mallotus villosus*) eggs daily to satiation. Capelin eggs are a convenient food source due to their consistency in size and mass and the ease with which they can be counted. Following acclimation, the fish were placed in individual aquaria and exposed to one of the three experimental treatments.

Characterizing intake rate curves

Quitting harvest rate theory assumes that, within a patch, foragers will experience a steadily diminishing energetic intake rate owing to food depletion (Brown, 1988, 1992). If this assumption is not met, and instead intake rate remains constant over time, fish would be expected to forage until all the food is consumed (Stephens and Krebs, 1986; Green, 1987). Under this scenario, the quitting harvest rate value would be meaningless because it would be the same regardless of experimental conditions, rather than differing as a function of patch-specific costs.

To test that the diminishing intake rate assumption was being met in this study, we conducted the following experiment. Individual fish were placed into the 20-litre experimental aquaria (0.21 ± 0.1‰ salinity and 10.9 ± 0.5°C) and left overnight to

acclimate. The following morning, 50 capelin eggs were placed in the vacant side of the aquaria. This both provided the fish with food and ensured that the fish had experienced this habitat. Three hours later, 50 eggs were placed in the opposite habitat (originally the preferred side) to ensure that the fish perceived equal food availability in both habitats. Most fish (72%) had returned to their preferred habitat, so were not required to switch a second time. At the end of the day, all remaining eggs were removed and counted. Fish that did not consume more than 50 eggs were not used in the second part of the trial. Fifty grams of brown and white mottled aquarium gravel was then scattered across each side of the aquaria. The addition of the gravel camouflaged the white capelin eggs, thus requiring the fish to search for them, and ensured that fish experienced a decreasing intake rate. The following morning (15 h later), 100 capelin eggs were dispersed over the gravel in whichever habitat the fish was not occupying, presumably its least preferred habitat in the absence of any food. Fish were then left to forage for 5 min ($n = 15$), 15 min ($n = 14$), 30 min ($n = 15$), or 60 min ($n = 12$). At the end of the trial, all remaining eggs were removed and counted to determine the average number of eggs eaten per time period.

Salinity experiments

In the salinity experiments ($n = 51$), one habitat was supplied continuously with freshwater (1.1 ± 1.1‰; 10.2 ± 0.5°C) and the other with saltwater (28.1 ± 0.6‰; 10.0 ± 0.4°C). At the beginning of the experiment, individual freshwater-acclimated fish were placed in the freshwater side of the aquaria and left overnight to explore. The following morning (15 h later), habitat preference was determined by observing the fish every 10 min for 90 min. Fish were observed by peering through slits in light occlusion blinds that provided a front view of the aquaria. The habitat in which fish spent ≥80% of their time was considered the 'preferred' habitat. The less preferred habitat was labelled the 'alternate' habitat. If preference was unknown after 90 min, the fish was excluded from the experiment. The remainder of the experiment followed the same procedure as the intake rate curve trials, except that fish were allowed to forage on the 100 eggs mixed with gravel in the alternate habitat until they decided to return to the preferred habitat. As soon as the fish returned to the preferred habitat, the remaining eggs were removed and counted. For each experiment the time spent in the alternate habitat and the number of eggs eaten was recorded. Fish that did not cross the divider to forage during the experiment were excluded from analysis, resulting in a final sample size of 44.

Temperature experiments

Two temperature experiments were conducted. In the first set of experiments (T4°C experiments, $n = 39$), the habitats differed by approximately 4°C (0‰ salinity, cold water 8.6 ± 0.3°C, warm water 12.6 ± 0.5°C). In the second set of experiments (T7°C experiments, $n = 41$), the habitats differed by approximately 7°C (0‰ salinity, cold water 8.9 ± 0.3°C, warm water 15.7 ± 0.3°C). To minimize temperature shock, the fish were introduced to the experimental aquaria when both habitats were 11.4 ± 0.6°C. Over a three-hour period, the two habitats were chilled or heated to experimental temperatures. Once the two habitats reached their experimental temperatures, the experiments followed the same procedure as the salinity experiments described above. Fish that did not cross the divider to forage during the experiment were excluded from the analysis, resulting in a final sample size of 35 in the

T4°C experiments and 39 in the T7°C experiments. Food rations during the temperature experiments were calculated based on feeding requirements in water of 8–9°C.

State variables

At the end of all salinity and temperature trials, fish fork length (FL), mass (M), and condition factor (CF) were recorded. Condition factor was calculated from fork length (to the nearest 0.1 cm) and mass (to the nearest 0.1 g) following McCormick and Naiman (1984):

$$CF = (M/FL^3) \times 100 \quad (1)$$

Subsequent to the salinity trials, we also measured gill Na^+/K^+-ATPase activity. Na^+/K^+-ATPase activity was measured on crude gill homogenates as outlined by McCormick (1993). Fish were killed by a blow to their head, and their gills were immediately removed, frozen in liquid nitrogen, and stored at −70°C. ATPase activity was normalized to total homogenate [protein] (measured using the bicinchoninic acid method with bovine serum albumin standards; Sigma-Aldrich). All samples were run in triplicate and the coefficients of variation were ≤ 10%. Ouabain-sensitive ATPase activity is expressed as micromoles of ADP per milligram of protein per hour.

We assume that Na^+/K^+-ATPase activity did not change significantly during the course of the two-day trials (Quinn *et al.*, 2003). As a result, individual differences in Na^+/K^+-ATPase activity are used as a predictor of fish habitat preference rather than a consequence of habitat use.

Data analysis

To estimate quitting harvest rates, we calculated the instantaneous intake rate of individual fish at the time of departure from the foraging habitat using the following procedure. First, the decline in intake due to diminishing prey density was described by fitting an intake rate curve to the data from the intake rate experiment. The intake rate curve that best described the data was of the form:

$$Y = a(1 - e^{-bt}) \quad (2)$$

where Y is the number of eggs eaten, t is the time spent foraging in the alternate habitat, a represents the maximum number of eggs available to be eaten ($n = 100$), and b is a shape constant. We then estimated the value of b for each fish in each experiment by fitting equation (2) to each fish's data on time in the alternate habitat and eggs eaten. The quitting harvest rate (or instantaneous intake rate) of each individual was estimated by evaluating the first derivative (dY/dt) of equation (2) given the time of departure from the alternate habitat. These estimates were translated into watts by multiplying by the caloric content of the eggs. The average egg weighed 0.065 g and was assumed to contain 0.249 $kJ \cdot g^{-1}$ (DeBlois and Leggett, 1993).

We used information theoretic methods (Sakamoto *et al.*, 1986; Akaike, 1992; Johnson and Omland, 2004) to asses the ability of the state variables to account for variation in the energetic costs of salinity and temperature. Information theoretic methods evaluate the relative strength of multiple models to explain the relationship between dependent and explanatory variables

by ranking models according to their fit to the data relative to the number of parameters in the model.

We first tested all 16 possible models containing linear combinations of salinity preference, Na^+/K^+-ATPase activity, fork length, and condition factor on quitting harvest rates associated with habitats varying in salinity, and tested all eight possible models containing linear combinations of temperature preference, fork length, and condition factor on quitting harvest rates associated with habitats varying in temperature. We then re-ran the analyses excluding preference. We excluded body mass from the analyses because it is highly correlated with fork length ($R^2 = 0.916$). Na^+/K^+-ATPase activity and length are also correlated ($R^2 = 0.434$); however, both factors were included in the analysis because the low R^2 value suggests much variation remains unaccounted for. The relative fit of each model was examined using Akaike's information criterion corrected for small sample size [AIC_c (Anderson *et al.*, 2000)]. A lower AIC_c value indicates a better approximation of the data set by a model. Akaike weights (w_i), an index of the strength of a model relative to all models considered, and the change in AIC_c between models (ΔAIC_c), were used to assess the strength of models as predictors of quitting harvest rate. The larger the ΔAIC_c, the less likely it is that a model is a good predictor of quitting harvest rate. The strength of individual state variables as predictors of quitting harvest rate is greater when the sum of Akaike weights for models containing that variable is high (ranges 0–1). The model average coefficient estimate of each variable (θ) and the unconditional standard error of θ provide the most precise information regarding the fit and statistical significance of a particular variable (Sakamoto *et al.*, 1986).

RESULTS

Intake rate curve

The assumption that foragers experience a steadily diminishing intake rate was met. The curve that best fit the intake rate data was an exponential rise to an asymptote (see equation 2) with b equal to 0.0598 ± 0.006 (mean ± standard error; $R^2 = 0.850$) (Fig. 4). Part of this deceleration in intake rate may be due to satiation; however, satiation could not have been

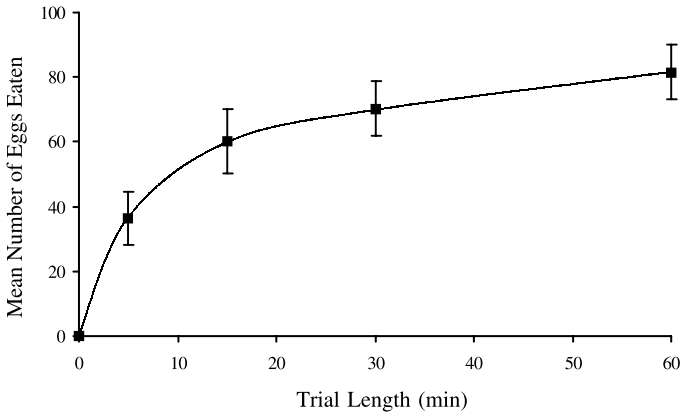


Fig. 4. Best-fit curve through the intake rate data on eggs eaten and trial length. Bars give the 95% confidence interval.

Table 1. Comparison of intake rates (parameter *b* in equation 2; see text) between intake rate trials (CI) and experiments conducted on various salinities and temperatures

Experiment	Contrasting intake rates	Significance
Salinity	ANOVA	$F_{2,75} = 15.636$, $P < 0.001$
	Tukey: SW < CI	$P = 0.005$
	FW < CI	$P < 0.001$
	SW > FW	$P = 0.026$
Temperature 4°C	ANOVA	$F_{2,66} = 5.701$, $P = 0.005$
	Tukey: CW < CI	$P = 0.023$
	WW < CI	$P = 0.017$
	CW = WW	$P = 0.999$
Temperature 7°C	ANOVA	$F_{2,70} = 5.436$, $P = 0.006$
	Tukey: CW = CI	$P = 0.081$
	WW < CI	$P = 0.010$
	CW = WW	$P = 0.245$

Note: SW = saltwater, FW = freshwater, CW = cold water, WW = warm water.

greater than 30%, as the fish were only given 100 eggs and preliminary feeding trials indicated that fish could eat more than 300 eggs. In any case, the actual mechanism is less important than the observed decline in intake rate.

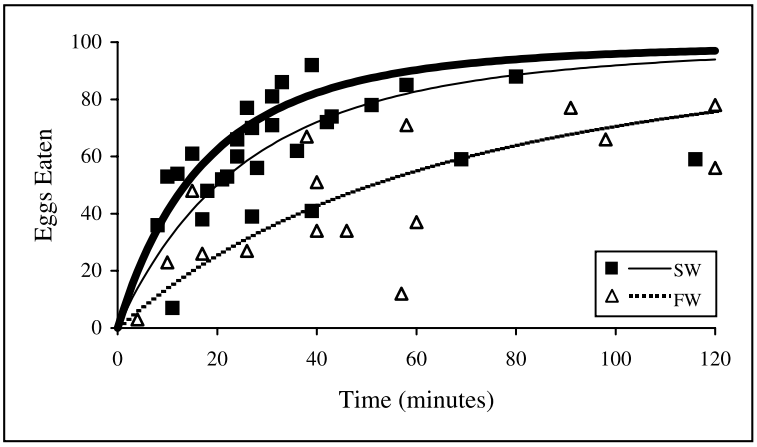
This parameter value cannot be used to estimate the quitting harvest rate of individual fish because intake rates (and thus values of *b*) varied both among and within experiments (Fig. 5). Values of *b*, estimated for individual fish, differed both between the experimental trials and from the intake rate trials (Table 1). The value of *b* was greater during the intake rate trials than for salt- and freshwater-preferring fish in the salinity experiments, cold and warm water-preferring fish in the T4°C experiments, and warm water-preferring fish in the T7°C experiments. In addition, intake rate was greater for saltwater-preferring fish than for freshwater-preferring ones (Fig. 5A). This variation in intake rate among experimental conditions indicates that intake rate is dependent on more than just prey density, thus supporting our use of quitting harvest rate rather than giving-up density.

Salinity experiments

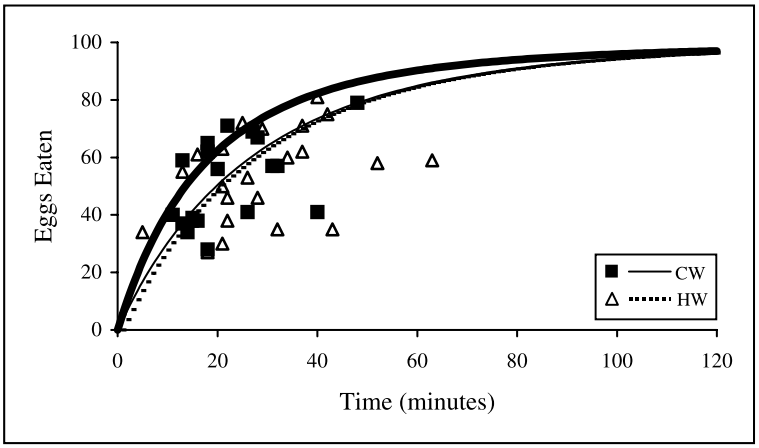
When given the choice between habitats of different salinity, more salmon preferred saltwater ($n = 33$) than freshwater ($n = 18$) ($\chi^2 = 4.412$, $P = 0.036$). Na^+/K^+-ATPase activity did not differ between the two groups ($F_{1,44} = 1.913$, $P = 0.174$). The quitting harvest rate, and

Fig. 5. A comparison of the intake rate of juvenile salmon during the intake rate curve trials (thick solid line) and experiments (dotted and thin solid lines). (A) Intake rate for saltwater-preferring (SW) fish and freshwater-preferring (FW) fish in the salinity experiment. (B) Intake rate for cold water-preferring (CW) fish and warm water-preferring (HW) fish in the T4°C experiment. (C) Intake rate for cold water-preferring fish and warm water-preferring fish in the T7°C experiment.

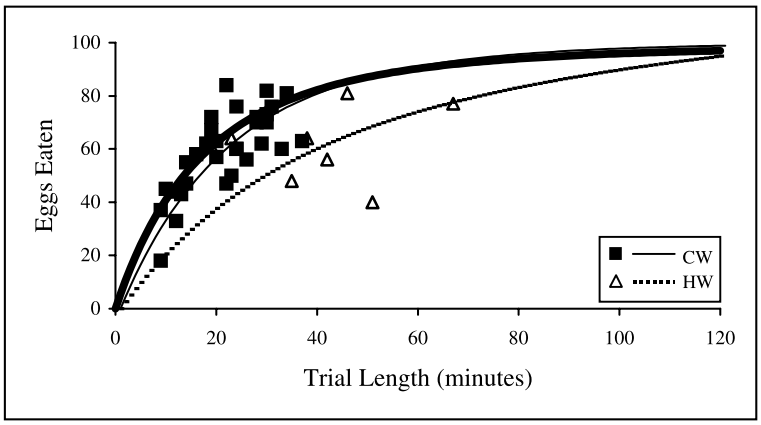
A. Salinity experiments



B. T4ºC experiments



C. T7ºC experiments



thus the energetic cost, of saltwater-preferring fish feeding in freshwater (0.361 ± 0.045 W; mean ± standard error) was 1.65 times greater than the quitting harvest rate of freshwater-preferring fish feeding in saltwater (0.218 ± 0.040 W) (ANOVA $F_{1,42} = 5.626$, $P = 0.022$). Consistent with the ANOVA results, the AIC analysis indicated that salinity preference was a significant predictor of quitting harvest rate. The model that best explained quitting harvest rate included salinity preference and fork length, but only explained 17.5% of the variation in quitting harvest rate. However, the sum of the Akaike weights for all models containing salinity preference was 0.92, indicating that preference was a robust predictor of quitting harvest rate. The role of preference as a predictor of quitting harvest rate was further supported by the model-averaged θ result, which indicated that the effect of preference on quitting harvest rate was statistically significant (0.26 ± 0.21 unconditional 95% CI).

When the AIC analysis was run on saltwater-preferring fish only, the best model for predicting quitting harvest rate included condition factor and Na^+/K^+-ATPase activity, but not fork length (Table 2). This model only explained 24.4% of the variation in quitting harvest rate; however, the sum of the Akaike weights for models containing the variables body condition and Na^+/K^+-ATPase activity were 0.68 and 0.70 respectively, indicating relatively high confidence that these variables were robust predictors of quitting harvest rate. In addition, the 95% confidence interval around the model-averaged θ indicated that the effect of Na^+/K^+-ATPase activity on quitting harvest rate was positive and statistically significant; however, the effect of body condition on quitting harvest rate was not significant (Table 3a).

AIC analyses of freshwater-preferring fish indicated that the best model for predicting quitting harvest rate included Na^+/K^+-ATPase activity only, but this model explained only 7% of the variation in quitting harvest rate (Table 2). In addition, the model-averaged θ for the effect of Na^+/K^+-ATPase activity on quitting harvest rate among freshwater-preferring fish was not significantly different from zero (Table 3b). In accordance with these findings, linear regression indicated that there was a significant interaction between the effects of

Table 2. Top four models of factors influencing quitting harvest rate of saltwater- and freshwater-preferring fish, as ranked by AIC_c

Models	K_i	ΔAIC_c	w_i	R^2
(a) Saltwater-preferring fish				
CF + Na^+/K^+-ATPase	3	—	0.422	0.244
FL	2	2.043	0.152	0.11
FL + Na^+/K^+-ATPase	3	2.609	0.114	0.17
FL + CF + Na^+/K^+-ATPase	4	2.726	0.108	0.245
(b) Freshwater-preferring fish				
Na^+/K^+-ATPase	2	—	0.382	0.07
FL + Na^+/K^+-ATPase	3	0.392	0.314	0.211
CF + Na^+/K^+-ATPase	3	1.738	0.160	0.142
FL + CF + Na^+/K^+-ATPase	4	2.609	0.104	0.278

Note: For each model i, K_i is the number of parameters in the model (including the constant), ΔAIC_c is the change in AIC_c between the model and the 'best' model (i.e. the model with the lowest AIC_c), and w_i is the Akaike weight. CF = condition factor, FL = fork length (see text).

Table 3. Estimates of effect on quitting harvest rate of factors included in models of saltwater- and freshwater-preferring fish

Variable	Σw_i	Model-averaged θ	Unconditional standard error (θ)	95% CI
(a) Saltwater-preferring fish				
FL	0.463	0.190	0.273	(–0.349 to 0.730)
CF	0.675	–0.211	0.147	(–0.50 to 0.077)
Na^+/K^+-ATPase	0.697	0.201	0.098	**(0.008** to **0.393)**
(b) Freshwater-preferring fish				
FL	0.428	0.802	0.693	(–0.557 to 2.161)
CF	0.273	–0.288	0.360	(–0.994 to 0.418)
Na^+/K^+-ATPase	0.961	–0.169	0.155	(–0.473 to 0.136)

Note: Σw_i is the sum of Akaike weights for all models containing a particular variable. The model average coefficient estimate of the variable θ is the average from all models containing that variable, weighted by each model's Akaike weight. The unconditional standard error of θ is a similarly weighted measure that incorporates both uncertainty in the coefficient estimate and uncertainty in the chosen model. The confidence interval was calculated using the unconditional standard error. **Boldface** 95% confidence intervals (CI) are significant because they do not encompass zero. CF = condition factor, FL = fork length (see text).

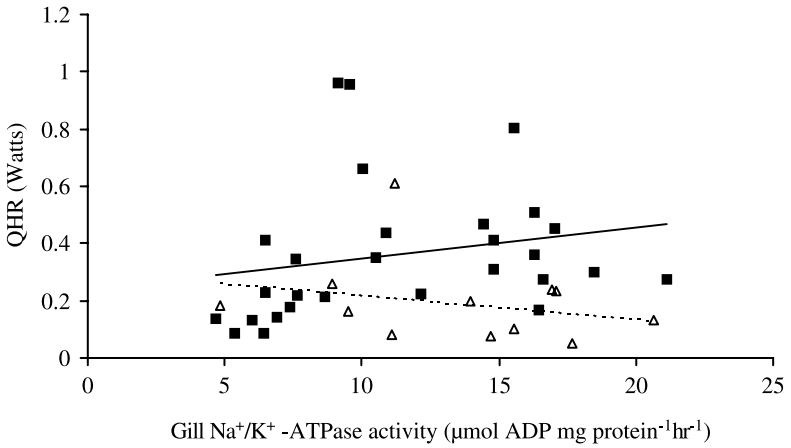


Fig. 6. Relationship between quitting harvest rate (QHR) and Na^+/K^+-ATPase activity for saltwater-preferring fish (squares and solid line) and freshwater-preferring fish (triangles and dashed line). The slopes of the regression lines are significantly different from one another ($P = 0.043$).

salinity preference and Na^+/K^+-ATPase activity on quitting harvest rate ($F_{1,37} = 4.410$, $P = 0.043$) (Fig. 6).

Temperature experiments

When given the choice between habitats that differed by 4°C (T4°C experiment), the same number of fish preferred cold and warm water ($\chi^2 = 0.026$, $n = 39$, $P = 0.873$), and quitting harvest rate did not differ between cold (0.451 ± 0.039 W; mean ± standard error) and warm

water-preferring fish (0.397 ± 0.058 W) (ANOVA $F_{1,39} = 0.541$, $P = 0.467$). However, when the difference in temperature between habitats was increased to 7°C (T7°C experiment), more fish preferred cold water ($n = 33$) to warm water ($n = 8$) ($\chi^2 = 15.244$, $n = 41$, $P < 0.001$), and the quitting harvest rate for cold water-preferring fish switching to warm water (0.471 ± 0.031 W) was 1.72 times greater than for warm water-preferring fish switching to cold water (0.274 ± 0.048 W) ($F_{1,37} = 11.824$, $P = 0.001$).

AIC analysis of the T4°C data indicated that none of the independent variables were correlated with quitting harvest rate. The best model explaining quitting harvest rate for the T7°C experiments included temperature preference, but accounted for only 24.2% of the variation in quitting harvest rate. However, the sum of Akaike weights for all models containing preference was 0.98, indicating high confidence that preference was a robust predictor of quitting harvest rate. In addition, the model-averaged θ indicated that the effect of preference on quitting harvest rate was statistically significant (–0.30 ± 0.18 unconditional 95% CI). These results are consistent with the ANOVA results.

When preference was removed as a factor from the AIC analysis, and the analysis was run on cold water-preferring fish from the T4°C experiments, the best model predicting variation in quitting harvest rate included fork length. However, this model explained only 16% of the variation in quitting harvest rate (Table 4) and the sum of Akaike weights for all models containing fork length was 0.44, indicating low confidence that fork length was a robust predictor of quitting harvest rate. In addition, the model-averaged θ indicated that

Table 4. Top four models of factors influencing quitting harvest rate of cold water-preferring fish in the 4°C experiments, cold water-preferring fish in the 7°C experiments, and warm water-preferring fish in the 7°C experiments, as ranked by AIC_c

Models	K_i	ΔAIC_c	w_i	R^2
(a) Cold water-preferring fish, 4°C experiment				
FL	2	—	0.347	0.16
Constant	1	0.374	0.288	—
CF	2	0.451	0.277	0.137
FL + CF	3	2.738	0.088	0.172
(b) Cold water-preferring fish, 7°C experiment				
FL	2	—	0.351	0.08
Constant	1	0.296	0.303	—
CF	2	1.320	0.181	0.04
FL + CF	3	1.512	0.165	0.108
(c) Warm water-preferring fish, 7°C experiment				
CF	2	—	0.485	0.017
FL	2	0.042	0.475	0.011
FL + CF	3	5.537	0.030	0.023
Constant	1	7.803	0.010	—

Note: For each model i, K_i is the number of parameters in the model (including the constant), ΔAIC_c is the change in AIC_c between the model and the 'best' model (i.e. the model with the lowest AIC_c), and w_i is the Akaike weight. CF = condition factor, FL = fork length (see text).

the effect of fork length on quitting harvest rate was positive, but not statistically significant (0.36 ± 0.49 unconditional 95% CI). None of the models explained a significant amount of the variation in quitting harvest rate for the warm water-preferring fish from the T4°C experiments.

For cold water-preferring fish in the T7°C experiments, the model that included fork length was the best predictor of quitting harvest rate. However, it only explained 8% of the variation in quitting harvest rate (Table 4), and the sum of Akaike weights for all models containing fork length was 0.52, indicating low confidence that length was a robust predictor of quitting harvest rate. The model-averaged θ indicated that the effect of fork length on quitting harvest rate was not statistically significant (0.27 ± 0.34 unconditional 95% CI). For the fish preferring warm water in the T7°C experiments, the best model for explaining variation in quitting harvest rate included either body condition or fork length, but both factors explained very little variation (1.7% and 1.1% respectively; Table 4c). The summed Akaike weights suggested that the probability that models containing either body condition or fork length were best among the set of models considered was 0.52 and 0.51 respectively. The model-averaged θ indicated that neither the effect of fork length nor body condition on quitting harvest rate was statistically significant (fork length: -0.07 ± 0.74 unconditional 95% CI; body condition: -0.13 ± 0.76 unconditional 95% CI).

Comparison across experiments

As discussed in the Introduction, a higher quitting harvest rate implies a higher energetic cost. Therefore, by comparing the quitting harvest rates associated with different environmental factors, differences in their relative costs can be assessed. Analysis of variance revealed significant differences in quitting harvest rate between experiments ($F_{5,118} = 6.143$, $P < 0.001$), but these differences were mostly due to the low relative cost of a change in salinity to freshwater-preferring fish compared to the higher relative cost of a change in temperature, particularly for cold water-preferring fish (Fig. 7).

DISCUSSION

Previous studies that have quantified costs associated with changes in salinity and temperature have focused on metabolic costs associated with one physiological mechanism rather than the total cost of occupying a habitat. The approach used here made it possible to measure the relative net costs of living in different abiotic conditions, thus providing us with a more complete understanding of how different abiotic conditions might influence juvenile salmon habitat choice and how habitat choices can change as a result of changes in the animal's state.

By defining all costs in common units of energy, we are now able to compare and contrast the energetic costs associated with different salinities to those associated with different temperatures. Such a comparison is of particular interest because as fish move through an estuary they are often confronted with sudden changes in temperature and salinity. In addition, in previous studies on juvenile salmon researchers have concluded that transition through estuaries is extremely stressful and risky, and they assigned the cause of this stress to adapting to increasing salinity (Järvi, 1989; Handeland *et al.*, 1996). Few, if any, studies of fish in estuaries have considered the stress and consequences of adapting to changes in temperature. Our results indicate that the energetic costs associated with differences in salinity

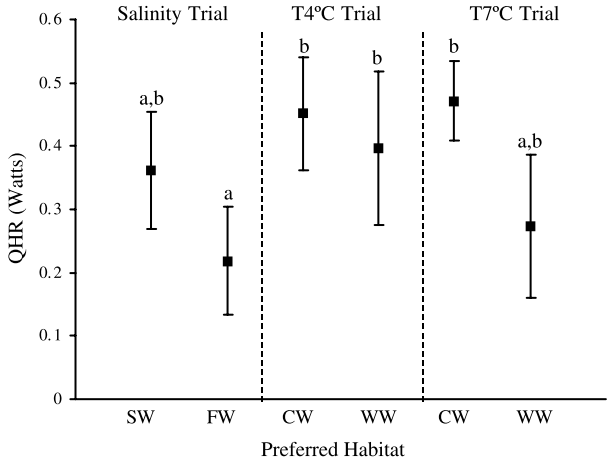


Fig. 7. A comparison of the quitting harvest rate (QHR) of saltwater (SW), freshwater (FW), cold water (CW), and warm water (WW) preferring fish during the three experiments. Values with the same letters were not significantly different (Tukey test: $P > 0.05$); values with different letters were significantly different (Tukey test: all $P \leq 0.014$).

and temperature, over the range we studied, are very similar to each other. The only exception was the low energetic cost experienced by freshwater-preferring fish foraging in saltwater. These results suggest that, if changes in temperature are sufficiently high, the effect of temperature on habitat choice by juvenile salmon may be equally, if not more, important than the effect of a change in salinity.

The energetic costs associated with different salinities and temperatures are not necessarily constant over time; rather, they can change as a result of changes in the salmon's state. Our results demonstrate that the energetic costs associated with residency in salt- and freshwater varied depending on the developmental stage of the fish. Fish that preferred saltwater habitats, and were at a more advanced developmental stage (high Na^+/K^+-ATPase activity), paid higher energetic costs when foraging in freshwater than did saltwater-preferring fish that were at an earlier developmental stage. This indicates that as salmon become more physiologically adapted for saltwater residency, the cost of returning to freshwater to forage increases. Surprisingly, the cost for freshwater-preferring fish to forage in saltwater was not related to their stage of physiological development, perhaps because we did not conduct trials on fish that had sufficiently low Na^+/K^+-ATPase activity. If the level of Na^+/K^+-ATPase activity below which fish have difficulty maintaining homeostasis in saltwater is lower than our lowest level (4.68 μmol ADP · mg protein^{-1} · h^{-1}), then we would not be able to detect the predicted negative relationship between Na^+/K^+-ATPase activity and energetic cost when foraging in saltwater (Fig. 1).

Although most fish in this study demonstrated a preference for saltwater, 35% of fish preferred freshwater, regardless of their Na^+/K^+-ATPase activity. This result indicates that it is not costly for fish with high Na^+/K^+-ATPase activity to reside in freshwater and, therefore, that the cost associated with elevated Na^+/K^+-ATPase activity is relatively low. This conclusion contradicts our finding that as Na^+/K^+-ATPase activity increases in saltwater-preferring fish, the energetic costs associated with foraging in freshwater increases. This may

be because other factors that change during smoltification, such as thyroid (Refstie, 1982) or prolactin (Brewer and McKeown, 1980) activity, may change in concert with Na^+/K^+-ATPase activity. Therefore, there may be salinity-related processes, other than Na^+/K^+-ATPase activity, which are causing increased energetic costs for saltwater-preferring fish to forage in freshwater.

The energetic cost incurred by saltwater-preferring salmon foraging in freshwater was 1.65 times greater than that of freshwater-preferring salmon foraging in saltwater, suggesting that it is significantly more costly for a saltwater-adapted fish to forage in freshwater than the reverse. This result cannot be directly compared with previous salinity-related cost estimates for several reasons. First, in contrast to studies that measure specific components of cost [e.g. metabolic costs (see Morgan and Iwama, 1998)], behavioural titrations measure total costs. Depending on how the different components that make up a cost interact, this could result in larger or smaller estimates than those estimated through traditional techniques. Second, previous energetic cost estimates have been made following acclimation to a new salinity rather than at the time of entry into a new salinity environment (Rao, 1967; Kirschner, 1993; Morgan and Iwama, 1998). However, when physiological changes are measured before acclimation to a new salinity, brief but large increases in cortisol, osmolarity, and plasma ion concentrations are recorded (Franklin *et al.*, 1992). These changes, particularly to cortisol (Morgan and Iwama, 1996; Mommsen *et al.*, 1999), likely result in increased energetic costs. The incorporation of these into our cost estimates could result in our estimates being higher than previous ones. Studies that have looked at the energetic costs associated with a change in salinity without acclimation have analysed the cost associated with moving from fresh- to saltwater (Franklin *et al.*, 1992) and not from salt- to freshwater. However, in estuaries, both types of changes in salinity often occur on short temporal and spatial scales. Our study is the first to quantify and compare the energetic cost of voluntarily moving between salinities in both directions.

Results from the temperature experiments indicated that when given a choice between 9 and 16°C, it was more costly for a fish to reside in warmer water. This result is consistent with what is known about the effects of temperature change on physiological parameters (Brett, 1971). When fish move into warm water their metabolic rate increases, and therefore the energetic cost of foraging in that habitat increases (Brett, 1971; Moffitt and Crawshaw, 1983). To cover the increase in metabolic costs, there must be sufficient food available. In the present study much of the fish's time was spent without food, and as a result the fish's preference for cold water could have been an attempt to reduce its metabolic costs.

Interestingly, when fish were given a choice between water of 8.6 and 12.6°C, they did not prefer the cooler water as expected. This could be related to the effects of both temperature shock and metabolic cost. Sudden increases in temperature, even if the habitat switch is voluntary, can result in an energetically costly shock response (Moffitt and Crawshaw, 1983; Clough *et al.*, 2002). In the present study, fish were acclimated to 11.4°C and then given a choice between a 1°C increase or a 3°C decrease in temperature. If fish are trying to reduce costs associated with temperature shock, they should prefer the warmer habitat where the temperature change is less. However, fish must also consider the benefit of residing in cooler water when there is limited food available. As a result, when choosing between water of 8.6 and 12.6°C, fish can either choose the warmer habitat where shock-related costs are reduced, or the cooler habitat where metabolic costs are reduced. The equal distribution of fish between the two habitats may therefore suggest that, at least in the short term, these costs are roughly equal.

Previously we noted how studies using the quitting harvest rate approach traditionally assume that a forager's intake rate is dependent only on prey density. As a result of this assumption, the food left in a patch at the time of departure (referred to as the giving-up density) is often used as a surrogate for quitting harvest rate (Brown, 1988) and the time to patch departure is not recorded. Because we suspected that changes in abiotic conditions might result in a change in intake rate, we decided to measure quitting harvest rate and not giving-up density. Had we not done this, our conclusions would have been different.

If we had analysed giving-up densities rather than quitting harvest rates, our results would have underestimated the cost of salinity by over 10%. This discrepancy occurs because the average intake rate decreased when fish had to switch salinity to forage. This decrease was greatest for fish that moved from fresh- to saltwater to feed than vice versa, and could have been due to a change in buoyancy. During the intake rate curve trials, both habitats were at 0‰ salinity; therefore, fish did not have to adjust their buoyancy when feeding in the alternate habitat. During the salinity experiments, fish either experienced an increase or a decrease in water density, and therefore buoyancy, as a result of a change in salinity. When fish moved from fresh to saltwater they became positively buoyant, which made it difficult for them to access the food at the bottom of the tank. The fish were observed trying to get to the bottom by increasing downward propulsion. The cost associated with this behaviour is unknown, but the fishes' ability to forage appeared to be compromised because they had difficulty staying on the bottom. As a result, the fishes' intake rate could have been significantly reduced. In contrast, when saltwater-preferring fish fed in freshwater they were negatively buoyant and therefore sank. To achieve neutral buoyancy, the negatively buoyant fish swam to the surface to gulp air. The cost of this in the shallow water of our aquaria would be quite low, and the fish could quickly resume foraging and maintain a fairly high intake rate.

The results of the T4°C experiments would not have changed significantly if giving-up densities were used instead of quitting harvest rates, but the T7°C experiment results would have. The number of eggs eaten (and thus giving-up density) in the warm and cold water during the T7°C experiments was not significantly different. However, warm water-preferring fish that foraged in cold water took twice as long to eat the same number of eggs as cold water-preferring fish that foraged in warm water. Results also indicated that all but the cold water-preferring fish in the T7°C experiments had intake rates that were less than those observed during the intake rate curve trials. A possible explanation for this decrease in intake rate is that the sudden change in temperature resulted in a temperature-shock response, since a known side-effect of shock is a reduction in intake rate (Jobling and Wandsvik, 1983; Schreck *et al.*, 1997).

In summary, the results of this study have confirmed previous physiological findings that the energetic costs associated with increasing salinity are positively correlated with developmental stage, but might involve factor(s) other than Na^+/K^+-ATPase activity. We have also demonstrated that the energetic cost experienced by saltwater-preferring smolts foraging in freshwater is similar to the energetic cost of cold water-preferring fish foraging in warm water. Although the results presented here are limited, in that they deal only with a small range of temperatures and salinities, we believe we have introduced a useful alternative to physiological methods for estimating the energetic costs associated with abiotic environmental variables. By applying this method to a range of salinities and temperatures, a more complete understanding of their effects on juvenile salmon

habitat choice will be developed. In addition, this method could be used to ascertain the effect of abiotic factors on the habitat decisions of a range of other organisms.

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