The effects of depth and salinity on juvenile Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) habitat choice in an artificial estuary

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The energetic cost for juvenile Chinook salmon *Oncorhynchus tshawytscha* to forage in habitats of different salinity and depth was quantified using a behavioural titration based on ideal free distribution theory. When given a choice between freshwater habitats of different depths (>0.83 or <0.83 m), a greater proportion of fish used the deeper habitat. When the deeper habitat was saltwater, the proportion of fish using it increased. When food was added to both the shallow freshwater and deep saline habitats, however, fish distribution returned to that observed when both habitats were fresh water. This indicates that the preference for deep saline habitats during the stratified phase was driven by some benefit associated with residency in deeper water, rather than salinity. The low perceived cost of low salinity might be in part due to the fish's ability to minimize this cost by only making brief forays into the alternate freshwater habitat. When the food ration delivered to the more costly, shallow habitat was 50% greater than that delivered to the less costly, deep habitat, fish distributed themselves equally between the two habitats, presumably because of equal net benefits. This study demonstrates that juvenile Chinook salmon prefer deep saline habitat to shallow freshwater habitats but will make brief forays into the freshwater habitat if food availability is sufficiently high. © 2007 The Authors

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Key words: depth; habitat choice; ideal free distribution; salinity; salmon.

INTRODUCTION

Juvenile salmonids migrating from their natal stream to the ocean pass through estuaries where they are confronted with spatial and temporal variation in abiotic factors, such as water depth, current, temperature and salinity. Various combinations of these factors are expected to result in different energetic costs and benefits for juvenile salmonids. Consequently, fishes must constantly assess

the costs and benefits of using different habitats to determine which one provides the greatest net benefit, and thus the highest fitness.

Changes to the costs and benefits of a habitat may alter its value relative to that of alternative habitats and may result in a change in the distribution of fishes among them. By experimentally altering the benefits (*e.g.* food availability) associated with a habitat, and evaluating the effect on fish distribution between habitats, it is possible to quantify differences in habitat cost. This method of quantifying cost is referred to as behavioural titration (Kotler & Blaustein, 1995) and is based on the concept that animals will leave a habitat if the net benefit of foraging there is below the net benefit of foraging in an alternate habitat (Brown, 1988). This prediction follows directly from the theory of ideal free distribution (Fretwell & Lucas, 1970). By calculating how much food must be added to the more costly habitat in order to equalize the net benefits of the two habitats, the difference in energetic cost between two habitats can be measured.

Behavioural titrations have been used to understand the distribution of drift feeding fishes as a function of cover (Grand & Dill, 1997; Giannico & Healey, 1999), predation risk (Gilliam & Fraser, 1987; Abrahams & Dill, 1989), competition (Grand, 1997; Grand & Dill, 1999) and temperature (Krause *et al.*, 1998; Hughes & Grand, 2000). Until recently (Webster & Dill, 2006), however, behavioural titration has not been used to quantify the influence of salinity on habitat preference even though changes in salinity are known to affect metabolic costs (Morgan & Iwama, 1991, 1998) and can result in osmotic stress (Yamashita *et al.*, 2003).

Webster & Dill (2006) used behavioural titration to quantify the energetic costs for young-of-the-year Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) to reside in habitats of different salinities. Their experimental protocol allowed Chinook salmon to choose between two horizontally stratified habitats with equal food but different salinities. This protocol provided a means for quantifying the energetic costs associated with habitats of differing salinities, but it did not incorporate the effect of water depth. Natural estuaries are typically stratified vertically, such that the less dense fresh or brackish water overlies the denser salt water. As a result of this stratification, fishes can choose between shallow and fresh or deep and saline habitats.

Shallow surface water is often considered to represent a more costly situation than deep water due to increased predation risk (Kramer, 1983; Collis *et al.*, 2001) and decreased foraging efficiency (Hughes & Dill, 1990). As a result, fishes given a choice between shallow and deep habitats should prefer the deep one. If, however, the osmotic cost paid by fishes to forage in salt water outweighs the benefit of residing in a deep habitat, they should choose a shallow freshwater habitat. Osmotic costs are, in part, dependent on Na^+K^+-ATPase activity, an enzyme that enables salmonids to eliminate excess salt through active ion transport (McCormick & Saunders, 1987). Na^+K^+-ATPase activity increases during downstream migration and upon entry into areas of increased salinity (McCormick *et al.*, 1985; Stefansson *et al.*, 2003). Fishes with lower enzyme activity (typically parr and fry) pay lower energetic costs in fresh water than in salt water and fishes with higher enzyme activity (typically smolts) pay lower energetic costs in salt water (Morgan & Iwama, 1991). Therefore, fishes

with lower osmotic costs in freshwater will have to trade-off the costs and benefits associated with water depth and salinity, whereas fishes with lower osmotic costs in salt water should always prefer the deep saline habitat.

To quantify the relative costs of deep saltwater habitats and shallow freshwater habitats to juvenile salmonids, a behavioural titration was used. Trials began with a comparison of the distribution of juvenile chinook salmon between two freshwater habitats of different depth that contained equal amounts of food. The deep-water habitat was then made saline to determine how this altered fish distribution. Finally, the difference in cost between the two habitats was estimated by calculating how much food had to be redistributed from the preferred to the less preferred habitat to equalize fish distribution (*i.e.* to equalize net benefits in the two habitats).

MATERIALS AND METHODS

FISH AND EXPERIMENTAL SET-UP

Experiments were conducted using young-of-the-year, ocean-type, Chinook salmon [mean ± s.e., fork length (L_F): 7·59 ± 0·07 cm, mass (*M*): 4·64 ± 0·13 g] that were obtained during April 2003 from Chilliwack Hatchery, Chilliwack, BC, Canada. Prior to use in experiments, fish were kept in a covered, outdoor, 2000 l flow-through tank maintained under natural photoperiod (49°13′ N) and continuously supplied with air-equilibrated well water (mean ± s.d., salinity 0 ± 0, temperature 11·99 ± 0·11° C and dissolved oxygen 90·58 ± 3·28% saturation). Fish were fed twice daily on a maintenance ration (2% biomass day^{-1}) of commercial salmon pellets (EWOS, Canada Ltd, Surrey, BC, Canada).

Trials were conducted in a water column simulator (WCS). The WCS is a clear Plexiglas™ 4500 l aquarium (height 2·40 m, width 2·40 m, breadth 0·80 m) with three, vertically separated water delivery loops that facilitate the formation of a horizontally flowing water column. The WCS is described in further detail in Birtwell & Kruzynski (1987) and Korstrom & Birtwell (2002). The water in the WCS was either completely fresh water or divided into two distinct habitats of unequal depth and salinity: a shallower freshwater habitat overlying a deeper saltwater habitat and separated by a narrow (9 cm) halocline (Fig. 1). Food (EWOS 1·5 mm dry fish food pellets) was delivered during daily 180 min foraging periods and arrived in separate allotments to the shallow and deep-water habitats *via* feeding tubes. Fish movement was observed through slits in vinyl curtains that enclosed the WCS and was continuously recorded by a low-light high-resolution camera (Panasonic Model WV-1850). Due to the narrowness of the halocline zone, it was arbitrarily decided to include fish using this zone with those in the freshwater zone. Because very few fish used the halocline zone (7% or mean ± s.d. 1·3 ± 0·4 fish) combining this zone with the freshwater zone had no qualitative effects on results compared to if it had been combined with the saltwater zone.

At the end of all trials L_F, *M* and the condition factor (*K*) were recorded. The value of *K* was calculated from L_F (nearest 1 mm) and *M* (nearest 0·1 g) following McCormick & Naiman (1984): $K = 100 \, ML_F^{-3}$

EXPERIMENTAL PROCEDURES

Trials were conducted between 1100 and 1440 hours on 13 groups of 20 fish that were of similar *M* (mean ± s.e. 0·85 ± 0·09 g) and L_F (mean ± s.e. 6·2 ± 0·5 mm). Trials consisted of four phases: acclimation (days 1 and 2), fresh water (day 3), stratified fresh and salt water (day 4) and titration (days 5 and 6). During each phase, the number of fish present in the two habitats was counted during eleven 20 min sample
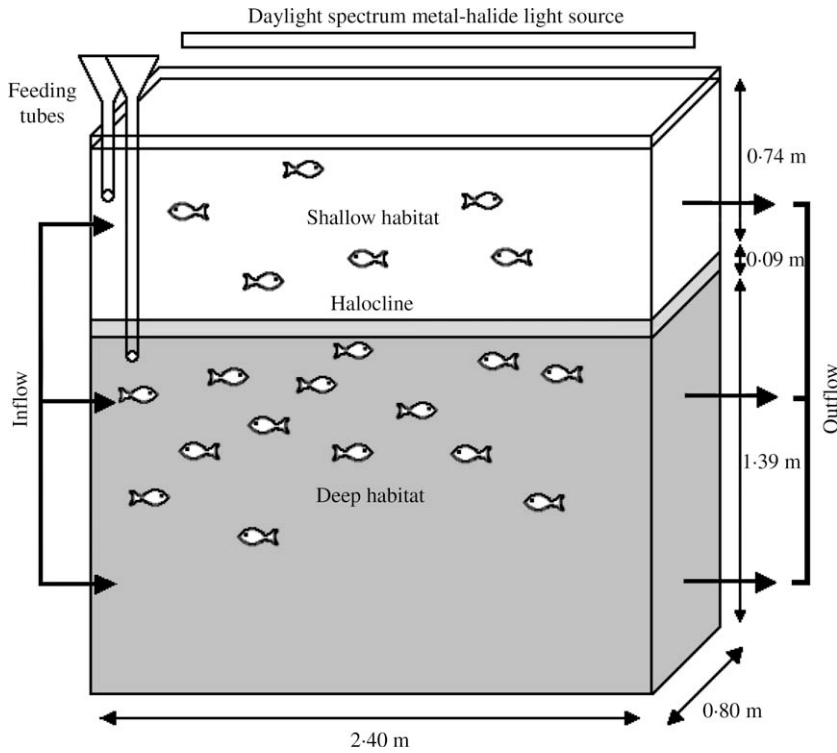
FIG. 1. Schematic representation of the water column simulator (WCS) apparatus. Water entered the WCS from the inflows and travelled at 0.3 m s^{-1}. The white shallow habitat contained fresh water throughout the experiments. The grey deep habitat was altered from fresh to salt water. The narrow halocline (light grey) was considered part of the freshwater habitat. Fish were free to move between the habitats.

periods. Each sampling period consisted of recording fish distribution every 30 s for 4 min followed by a 16 min pause. Each phase consisted of pre-foraging and foraging stages, with four and seven sample periods respectively.

During the acclimation and freshwater phases, both habitats were supplied with freshwater and equal amounts of food (see Table I for water conditions during all phases of the experiment). During the stratified phase, food availability remained equal, but the deeper habitat was salt water. On completion of the stratified phase, fish distribution

TABLE I. Summary of water quality (mean ± S.D.) in the two habitats of the water column simulator during the four trial phases

Trial condition	Habitat	Salinity	Dissolved oxygen (% air saturation)	Temperature (° C)
Acclimation/fresh water	Shallow	0·16 ± 0·12	99·80 ± 2·13	10·13 ± 0·04
	Deep	0·10 ± 0·08	99·11 ± 2·95	10·17 ± 0·10
Stratified/titrations 1 and 2	Shallow	1·20 ± 0·79	99·51 ± 2·14	10·16 ± 0·03
	Deep	26·17 ± 5·35*	97·50 ± 3·16	10·14 ± 0·10

*This is the condition that was changed between the acclimation/freshwater and the stratified/titration phases of each trial.

data were used to estimate the energetic cost (E) of the shallow freshwater habitat, relative to the deep saltwater habitat. To do this, the difference in the intake rate of individuals in the preferred habitat (that chosen by the majority of the fish) relative to those in the alternate habitat (that chosen by the minority of the fish) was calculated (Webster & Dill, 2006).

The objective of the titration phase was to test if the estimate of E was accurate. In this phase, the water column remained vertically stratified, but food availability was no longer equal between habitats. Food availability was determined by calculating how the total amount of food should be distributed between the preferred and alternate habitats in order to offset the high energetic cost of the alternate habitat and thus equalize the net benefits of the two habitats. Thus, the amount of food in the alternate habitat was greater than that in the preferred habitat.

During the titration phase, fish distributions were recorded, under the new food distribution conditions, on both day 5 (titration 1) and day 6 (titration 2) of each trial. The movement of fish to a 50:50 distribution (10 fish in each habitat) would suggest that a fish's estimate of the value of the habitat is a linear additive function of food benefits and abiotic costs (Abrahams & Dill, 1989). Prior to data analysis, all proportions were arcsine square-root transformed to ensure normality.

DEVELOPMENTAL STAGE

The energetic cost associated with foraging in water of different salinities is dependent on the developmental stage of the Chinook salmon, which can be determined by measuring gill Na^+K^+-ATPase activity. The gill Na^+K^+-ATPase activity of 10 fish per trial was measured using crude gill homogenates as outlined by McCormick (1993). Fish were killed with a blow to the head after which their gills were dissected and immediately frozen in liquid nitrogen and subsequently stored at $-70°$ C. ATPase activity was normalized to total homogenate (protein) (measured using the bicinchoninic acid method with bovine serum albumin standards; Proliant Inc., Ankeny, IA, U.S.A.). All samples were run in triplicate and the coefficients of variation (CV) were $\leq 10\%$. Ouabain-sensitive ATPase activity is expressed as μmol ADP mg^{-1} protein h^{-1}. Fish from trials where there was a strong preference for salt water during the stratified phase would probably have higher mean Na^+K^+-ATPase activity.

RESULTS

During the pre-foraging stage more fish used the deep habitat in both the fresh water and stratified phases of the trials (paired t-test, both d.f. = 12, $P < 0.001$). Significantly more fish, however, occupied the deep habitat during the stratified phase (68·5%) than during the fresh water phase (60·3%) (Fig. 2; paired t-test, d.f. = 12, $P < 0.05$). During the foraging stages, fish again used the deep habitat more than the shallow habitat in both the fresh water and stratified phases (paired t-test, both $P < 0.001$) but, in contrast to the pre-foraging stages, the distribution of fish did not differ between freshwater and stratified phases (Fig. 2; paired t-test, d.f. = 12, $P > 0.05$).

It was calculated that $60 \pm 2\%$ (mean $\pm$ S.E.) of the food must be present in the shallow freshwater habitat (or 50% more than in the deep habitat) in order to offset the higher cost associated with foraging there. The addition of this amount of food to the shallow freshwater habitat did result in an equal distribution of fish between habitats during titration 2 (Fig. 3; paired t-test, d.f. = 12, $P > 0.05$), but not during titration 1 (paired t-test, d.f. = 12, $P < 0.05$). In titration 1, however, fish did move in the predicted direction (*i.e.* some fish moved from the deep saltwater habitat to the shallow freshwater habitat).
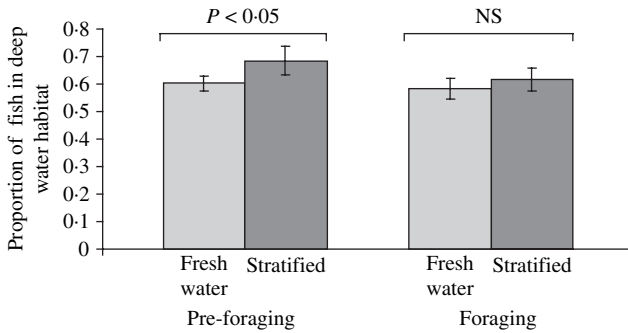
FIG. 2. The mean ± 95% CI proportion of juvenile Chinook salmon using the deep-water habitat during pre-foraging and foraging stages of the freshwater and stratified phases. A significant P-value denotes a difference in the number of fish in the deep habitat between phases. NS, non-significant.

The mean ± S.E. gill Na^+, K^+-ATPase activity level was $11\cdot15 \pm 0\cdot27$ µmol ADP mg $protein^{-1}$ h^{-1} (range: $8\cdot93$–$13\cdot01$ µmol ADP mg $protein^{-1}$ h^{-1}). The change in preference for the deep habitat between the fresh water and the stratified phases was not correlated with L_F, K or Na^+, K^+-ATPase activity (linear regression, $F_{3,9}$, $P > 0\cdot05$).

DISCUSSION

When given a choice between two habitats that differ in water depth, a greater proportion of juvenile Chinook salmon smolts used the deeper habitat. When salt water was then added to the deeper habitat to mimic the vertical stratification of an estuary, the proportion of fish using the deeper habitat increased. This preference for salt water is consistent with what is expected of fish at this developmental stage (fish with Na^+, K^+-ATPase activity levels of $11\cdot15$ µmol ADP mg $protein^{-1}$ h^{-1} typically prefer salt water; Beckman & Dickhoff, 1998; Negus, 2003). These results indicate that the net benefit for smolts to reside in a deep-water habitat ($>0\cdot83$ m) is greater than that in a
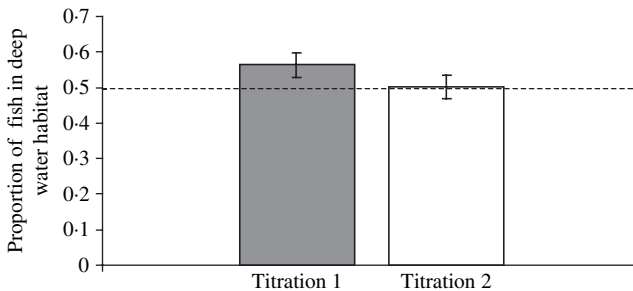

FIG. 3. The mean ± 95% CI proportion of juvenile Chinook salmon using the deep (v. shallow) water habitat during the foraging stages of titrations 1 and 2. Titration 2 resulted in fish returning to an equal distribution between habitats (i.e. number of fish in the deep habitat was not significantly different from 50%, as represented by the dashed line).

shallow-water habitat (<0·83 m) and that the net benefit is increased if the deep habitat is saline.

The addition of food to both habitats during the stratified phase resulted in the return of the fish distribution to that observed during the freshwater phase. This result was surprising as it indicates that, although smolts prefer salt water, the energetic cost of foraging in fresh water is negligible. This finding is inconsistent with the results of Webster & Dill (2006), who showed that foraging in fresh water was 69·7% more costly than in salt water. This discrepancy between the two studies is probably because different experimental set-ups resulted in different foraging tactics. In the present study, resources were temporally clumped, population density was relatively low and resource density was low because water current caused food to disperse immediately upon entering the habitat. These conditions characterize an environment in which the net benefit of scramble competition most probably exceeded the net benefit of resource defence (Grant, 1993). Therefore, fish maximized their net gain by scrambling for the food when it arrived and residing in the less costly saltwater habitat in the interim. The energetic cost of a short foray into the freshwater habitat would probably be relatively low as there would be a lag before the fish's physiological processes respond to the new osmotic conditions and because energetic requirements to maintain osmotic balance is a function of time spent in fresh water. Fish were frequently observed moving back and forth between habitats during foraging trials and exhibiting low levels of aggression and resource defence behaviour. The previous study by Webster & Dill (2006) followed the same procedures as the current study, however, their use of a much smaller experimental apparatus resulted in higher population density and a spatially predictable, non-depletable food resource. Under these conditions, resource defence is probably the most economical foraging strategy (Grant, 1993). Consequently, when resources are defendable, obtaining food in freshwater requires fish to defend a territory there and, as a result, pay the full cost of freshwater residency. When resources are not defendable, however, fish can reside in salt water and make brief forays into the more costly freshwater habitat when food is present and, therefore, pay only a short-term freshwater residency cost.

It was calculated that the energetic cost to forage in the shallow freshwater habitat was 50% higher than that in the deep saltwater habitat. This calculation of cost was verified when, in titration 2, the re-distribution of food between the shallow and deep-water habitats induced fish to pay the higher cost associated with the shallow freshwater habitat and resulted in fish moving to an equal distribution. The fresh and saltwater habitats differed in water volume; however, it is unlikely that this influenced fish distribution for two reasons. First, food was dispersed to the upper half of both habitats and was consumed before it sank to the deeper habitat or to the bottom of the WCS. As a result, food was restricted to similar volumes of water in both habitats. Second, few fish used the bottom half of the deep habitat, an observation that is consistent with a previous study using this apparatus (Birtwell *et al.*, 2003).

This experiment was not designed to determine why fish prefer one water depth to another; however, there are some possible explanations for further study. Water depth preference has been related to foraging efficiency (Clark & Levy, 1988) and predator avoidance (Eggers, 1978; Clark & Levy, 1988;

Appenzeller & Leggett, 1995). In the present study, water temperature, velocity and dissolved oxygen were equal between the two habitats and, therefore, abiotic factors are unlikely to have had an effect on the depth preference of the fish. Perceived predation risk may have affected depth preference (Gregory, 1994; Krause *et al.*, 2000), but hatchery-reared fishes are predator naïve and have been shown to have impaired predator avoidance abilities (Dieperink *et al.*, 2001; Einum & Fleming, 2001). Alternatively, depth preference may have been affected by foraging efficiency, which depends on search and handling costs (Holling, 1959). For instance, juvenile salmonids may be better able to detect prey by swimming below them and taking advantage of the visual contrast of the prey against the bright water surface (Galbraith, 1967; Novales-Flamerique, 2000). In addition, attacks on prey are often concentrated within an angular window in front of the fishes (Lythgoe, 1979; Richmond *et al.*, 2004); therefore, by being deeper in the water column salmonids may have a larger window for prey detection.

In summary, Chinook salmon smolts in this experiment preferred deeper saltwater habitats to shallow freshwater habitats. It is the net benefit associated with residency in deep habitats and not water salinity, however, that drives this preference. The increased cost associated with foraging in shallow water can be offset if there is 50% more food available there than in deep water. Salinity related costs would probably have been greater, if fish were not able to minimize them by making only brief forays into fresh water to forage when food was present. Based on the similarity of the stratified WCS to a natural estuary, however, the back-and-forth behaviour between the fresh and saltwater habitat may well be representative of fish behaviour in the wild.

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