

RESEARCH ARTICLE

Oxygen consumption of drift-feeding rainbow trout: the energetic tradeoff between locomotion and feeding in flow

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ABSTRACT

To forage in fast, turbulent flow environments where prey is abundant, fishes must deal with the high associated costs of locomotion. Prevailing theory suggests that many species exploit hydrodynamic refuges to minimize the cost of locomotion while foraging. Here, we challenge this theory based on direct oxygen consumption measurements of drift-feeding trout (*Oncorhynchus mykiss*) foraging in the freestream and from behind a flow refuge at velocities up to 100 cm s⁻¹. We demonstrate that refuging is not energetically beneficial when foraging in fast flows because of a high attack cost and low prey capture success associated with leaving a station-holding refuge to intercept prey. By integrating optimum foraging theory with empirical data from respirometry and video tracking, we developed a mathematical model to predict when drift-feeding fishes should exploit or avoid refuges based on prey density, size and flow velocity. Our optimum foraging and refuging model provides new mechanistic insights into locomotor costs, habitat use and prey choice of fish foraging in current-swept habitats.

KEY WORDS: Swimming, Flow refuging, Kármán gait, Prey capture, Turbulence, Respirometry, Ecology, Behavior

INTRODUCTION

The mechanisms underlying how animals distribute themselves in nature are a topic of major interest to ecologists. One major tenet is that animals seek to maximize their fitness by optimizing the ratio of energy intake to energy usage. In current-swept environments, fish distribute themselves by exploiting flow refuges and vortices to reduce the cost of locomotion (Cotel et al., 2006; Liao et al., 2003a; Johansen et al., 2008; Wilkes et al., 2017). These habitats are also often associated with high prey density (Hill and Grossman, 1993; Hayes et al., 2007; Jenkins and Keeley, 2010). Theoretical cost-benefit models assert that the distribution pattern of fish, which may vary between direct flow exposure and more sheltered refuge positions (e.g. Hughes and Dill, 1990; Piccolo et al., 2014), reflects their attempt to minimize energy used for swimming while maximizing their energy intake through foraging (Kiflawi and Genin, 1997; Rosenfeld et al., 2014; Piccolo et al., 2014). However, as empirical data on the cost of foraging are non-existent, these models are prone to prediction inaccuracies.

Here, we developed a data-driven energetics model that predicts fish foraging strategy and prey size as a function of flow velocity. This approach enabled us to address previously inaccessible questions such as: (1) what is the ability of refuging fish to detect and capture prey? (Rosenfeld et al., 2014); (2) what are the direct energetic costs of leaving a refuge to capture prey? (Guensch et al., 2001); and (3) what is the optimum foraging and refuging strategy? We tested the long-standing hypothesis that foraging fish expend less energy when refuging compared with swimming in the freestream. By directly measuring oxygen costs of foraging fish, we demonstrate that fish foraging in fast flow do not gain an energetic benefit when refuging.

MATERIALS AND METHODS

Animals

We selected rainbow trout *Oncorhynchus mykiss* (Walbaum) as a common, representative drift-feeding species. Fish were obtained from the Chattahoochee Forest National Fish Hatchery, GA, USA, and the Cantrell Creek Trout Farm, NC, USA. Fish were kept in two 473 l circular freshwater tanks maintained at 15±0.5°C (mean±s.e.m.) with a DS-4-TXV Delta Star Chiller (Aqua Logic Inc., San Diego, CA, USA). The fish were kept on a 12 h:12 h light:dark cycle and fed commercial trout pellets daily for a minimum of 1 week prior to experimentation (Pentair Dense Culture F2A Pellets).


Trout were divided among two experimental treatments: 14 large trout (mean±s.e.m. total length 33.0±0.6 cm, mass 423.8±19.2 g) were used to measure oxygen consumption and energy expenditure while swimming, which requires a relatively small volume of water to fish size for accuracy (generally less than 300:1 by volume) (Clark et al., 2013; Svendsen et al., 2016); 18 smaller trout (total length 16.3±0.2 cm, mass 70.3±4.3 g) were used to measure prey detection and capture success. For these experiments, it was important that fish had enough space in the experimental flow tank to maneuver and capture drifting prey unconstrained (see below). Trials were conducted within the 12 h daily light regime in order to match the diurnal activity of the study species, and all test subjects were starved for 48 h before the start of experiments to maximize feeding motivation and to ensure a post-absorptive state for swimming (Niimi and Beamish, 1974). All protocols were approved by the University of Florida Institutional Animal Care and Use Committee.

Experimental setup

All experiments were conducted using a customized 175 l recirculating flow tunnel respirometer (Loligo Systems) with a working section of 25×26×87 cm (width×depth×length). Flow within the working section of the respirometer was calibrated from 0 to 145±0.5 cm s⁻¹ (mean±s.e.m.) using digital particle image velocimetry (DPIV, 5 W argon-ion continuous laser, LaVision software). Water within the system was filtered, fully aerated and maintained at a temperature of 15±0.1°C (mean±s.e.m.) using a thermostat (Auber Instruments TD-100A) attached to a chiller

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(Aqua Logic DS-4). A 5 cm diameter, D-section cylinder was placed in the front of the working section to generate a distinct flow refuge within the sealed respirometer (characterized in Liao et al., 2003b) that provided unsteady flows similar to those that fish may experience in the wild (reviewed by Liao, 2007). A Phantom V12 high speed video camera (1024×1024, 150 frames s⁻¹, Vision Research) was aimed at a mirror angled at 45 deg below the working section to record the swimming kinematics and feeding behavior of individual trout. In all trials, solid blocking effects of the fish in the working section were corrected following Bell and Terhune (1970) and never exceeded 5%.

Oxygen consumption measurements

Oxygen consumption was used as a measure of the energetic cost of locomotion. Individuals were introduced into the respirometer and left to acclimatize overnight (10–12 h) at a current velocity of 0.5 L s⁻¹, where L is the total body length (i.e. 16.5 cm s⁻¹), until oxygen consumption had reduced to a steady state level and the fish had settled into a continuous swimming rhythm. The trial was then started and oxygen consumption was measured at increasing current velocities from 0.5 to 3.0 L s⁻¹, in 0.5 increments (i.e. 16.5–100.0 cm s⁻¹). Oxygen consumption at each velocity was determined over three consecutive 16 min measurement cycles. The treatment order in which fish were tested (swimming with no cylinder or refuging behind a cylinder) was randomized. We defined the maximum current velocity as the velocity when fish could no longer hold position and were swept onto the downstream grid for longer than 5 s. The experiments were then stopped and the current velocity returned to 16.5 cm s⁻¹. The cylinder was then either removed or added depending on the previous treatment, and the fish was left to recover overnight. The experimental protocol was repeated the next morning. After data were collected for each fish both refuging and swimming in the freestream, the trial was ended and the fish was returned to its holding tank.

For every oxygen measurement cycle, a 300 s flush, 60 s equilibration and 600 s measurement period was applied following the intermittent flow respirometry methodology of Steffensen et al. (1984) and Steffensen (1989). The flushing period ensured the oxygen concentration throughout the trial did not decrease below 85% of air saturation and avoided any CO₂ build up. Oxygen levels within the swimming respirometer were measured using a D901 miniature galvanic dissolved oxygen probe (Qubit Systems, Kingston, ON, Canada) and monitored with Autoresp v.1.6 software (Loligo Systems). To reduce bacterial growth and respiration within the system, the respirometer was regularly treated with a Clorox solution and thoroughly flushed with freshwater. This procedure ensured background respiration remained below 3% of the oxygen consumed by each fish during swimming trials, which was subtracted from the overall oxygen consumption of the subject. Specifically, after the fish had been returned to its holding tank, the respirometer was run for two additional 16 min measuring cycles at 33 cm s⁻¹ during which the reduction in oxygen saturation in the empty respirometer was measured.

Energetic cost of attack

We modified our respirometry protocol to measure the energetic cost of attack. The same flush, equilibrium and measuring periods were used as above; however, to avoid significant increases in oxygen consumption due to digestion (i.e. specific dynamic action, SDA; Alsop and Wood, 1997), a 2 mm artificial food particle (herein referred to as the lure) was constructed from synthetic yarn wrapped onto a size 20 fishing hook with the hook point cut off at

the bend. The lure enabled examination of the energetics of foraging attempts without the interference associated with the cost of digestion. Thin fluorocarbon line (2 lb test) was tied to the lure so that it could be introduced into the respirometer through small access ports located upstream of the cylinder. This allowed repeated trials of drifting the lure naturally with the current towards the test subject. To ensure the lure smelled like food, prior to each experiment it was soaked for 1 h in 200 ml sterilized water containing 30 commercial trout food pellets (Pentair Dense Culture F2A Pellets).

At the beginning of a trial, each fish was randomly assigned to an initial ‘no-cylinder’ or ‘cylinder’ treatment. The fish was then introduced into the respirometer and left to acclimatize overnight at a current velocity of 16.5 cm s⁻¹ until oxygen consumption had reached a steady-state level and the fish had settled into a continuous swimming rhythm (~12 h). Current velocity was then gradually increased to the experimental velocity of 68.0 cm s⁻¹ at a rate of 0.2 cm s⁻². The fish was left to acclimate for 2–4 h at this speed until oxygen consumption rate stabilized.

Feeding responses were stimulated by introducing water scented with food into the flow tank through 1.0 cm diameter access ports. After 1 min, the tethered lure was randomly injected into the flow tank through one of three access ports and allowed to drift passively in the freestream flow towards the fish. This procedure enticed the fish to attack the lure, and we recorded the number of attacks as well as the number of times that the fish ignored the lure. Whenever the lure was successfully captured or had passed the fish, it was immediately retracted back to the point of entry by swiftly pulling on the line. After 10 s, the lure was re-introduced randomly into the flow tank. We repeated this procedure throughout the 600 s oxygen consumption measuring period, which allowed fish to perform attacks *ad libitum* ($n=14$ fish). We were able to measure oxygen consumption across a wide range of attacks because of the inherent variability in behaviors across individuals. Note that we measured cost of attack at one flow speed, and assumed that it increases proportionally with speed (see also Godin and Rangeley, 1989).

Measuring probability of prey capture success

Energy intake trials did not rely on respirometry and could therefore take advantage of real food particles. Prior to these feeding trials, 30 small (3 mm) trout food pellets (Pentair Dense Culture F2A) were soaked in 200 ml sterilized water for an hour and then individually sectioned in two to minimize satiation of the fish during the trial. Small (3 ml) pipettes were then filled with either scented water containing no food or scented water containing food (hereafter referred to as a food particle). All samples of scented water and food particles were then kept in a temperature-controlled bath and used within 1 h of preparation. Capture success was defined as the number of captured prey divided by the number of attacks.

Experimental treatment and acclimatization protocols were similar to those of the respirometer trials above. Briefly, the fish was introduced into the flow tank and left to acclimatize for 2–4 h until it had settled into a continuous swimming rhythm (flow velocity 16.5 cm s⁻¹). The flow velocity was then slowly increased at a rate of 0.2 cm s⁻² to one of five experimental velocities (16.5, 33, 51, 68 or 84 cm s⁻¹). Once the target velocity had been reached, fish were left to acclimate for another 5 min. After 1 min of exposure to food-scented water, the first food particle was injected into the flow tank. For each food particle injected, we recorded whether the fish: (1) showed no reaction or (2) attempted to capture the particle, defined as a clear change in direction towards the particle. Capture movements were further divided into successful and failed attempts.

These capture behaviors (ignore, successful, failed) were recorded until a total of five successful captures were observed. At this point, the feeding trial was paused and another current velocity randomly selected. The trial was repeated until each fish had been examined at each of the five experimental flow velocities. This procedure allowed each fish to consume a maximum of 25 food particles, which was equivalent to less than 1% of fish body mass.

Experimental data analysis

The energetic cost of locomotion (for both cylinder refuging and freestream swimming) was plotted as oxygen consumption (\dot{M}_{O_2} , mg O_2 kg^{-1} h^{-1}) versus swimming speed ($cm\ s^{-1}$) and fitted with a three-parameter non-linear power function ($y=a+bc^x$, where $a+b$ is the y -axis intercept) following Roche et al. (2013). Differences in oxygen consumption between groups were analyzed using repeated measures ANOVA and swimming speed as a fixed factor. The energetic cost of attack (for both refuging and freestream swimming) was presented as oxygen consumption of individuals plotted against attack rate per hour, where an attack is defined as a sudden change in direction of the head to intercept the lure. A linear regression was fitted to these data and the slope was used to derive the combined anaerobic and aerobic cost of attacking a single drifting food particle. The difference in slopes was compared using an analysis of covariance (ANCOVA), with refuging behavior and current velocity as categorical and continuous variables, respectively. We converted energetic cost values from mg O_2 kg^{-1} h^{-1} to joules using a conversion rate of 1 mg $O_2=13.56$ J (Elliott and Davison, 1975).

Prey detection was defined as the proportion of food particles that a fish attempted to capture per unit time, and was fitted with a best-fit quadratic polynomial curve ($y=ax^2+bx+c$, where c is the y -axis intercept). Differences in prey detection rate between refuging and freestream swimming fish were compared using a two-way ANOVA with refuge/freestream swimming and current velocity as fixed factors, followed by a Tukey HSD *post hoc* test to identify differences between groups.

Prey capture success was defined as the proportion of food particles that was successfully ingested. Capture success was plotted against flow velocity and fitted with a best-fit three-parameter sigmoidal curve [$y=a/(1+\exp^{-(x-x_0)^b})$, where a , b and x_0 are constants]. Differences in capture success between refuging and freestream swimming fish were evaluated using a two-way ANOVA with refuge/freestream swimming and flow velocity as fixed factors, followed by a *post hoc* planned comparison for specific differences between groups and corrected for type I errors using false detection rate (Benjamini and Hochberg, 1995).

Cost-benefit model

We developed a mathematical model to estimate the conditions that would provide the greatest net energy gain (E_{Net}) in drift-feeding fish, focusing specifically on: (a) optimum flow velocity; (b) optimum use of refuges; and (c) required prey size and density versus flow velocity. Note that capitalized alphabet letters appearing in bold throughout the text and equations refer to variables in Tables 1 and 2. Estimates of E_{Net} of foraging fish in flow streams were based on gained (E_{Gain}) and lost (E_{Cost}) energy over 1 h periods:

$$E_{Net} = E_{Gain} - E_{Cost}. \quad (1)$$

We defined E_{Gain} and E_{Cost} as:

$$E_{Gain} = \mathbf{U} \times P_{Capture} \times \mathbf{J} \times E_{Prey}, \quad (2)$$

$$E_{Cost} = E_{Locomotion} + \mathbf{U} \times E_{Attack}, \quad (3)$$

where \mathbf{U} is the number of attacks, $P_{Capture}$ is the probability of prey capture success and \mathbf{J} is a variable taken to describe the percentage of prey energy available to fish after accounting for digestion and excretion (0.68; Hill and Grossman, 1993). E_{Prey} is the energy content of an invertebrate prey (in joules), which is described as a function of prey size after Jenkins and Keeley (2010):

$$E_{Prey} = 0.3818 \times \mathbf{D}^{2.46}, \quad (4)$$

where \mathbf{D} is the diameter of prey (in mm), and $E_{Locomotion}$ and E_{Attack} are the energetic cost of swimming and attacking prey, respectively. See Tables 1 and 2 for a complete description of model parameters, formulae and data acquisition.

Cost-benefit model analysis

First, we used the cost-benefit model to calculate net energy gain (for both refuging and freestream swimming) over a range of flow velocities (2.0–100 $cm\ s^{-1}$, in 1.0 $cm\ s^{-1}$ increments) and number of attacks (1– \mathbf{U}_{max}). For each experiment, \mathbf{U}_{max} changed dynamically depending on prey availability and eating capacity of fish. Note that the maximum number for \mathbf{U}_{max} per hour was 720 as we assume that each prey attack lasted 5 s (Bachman, 1984). Prey availability was calculated as:

$$\text{Prey availability} = \mathbf{B} \times \mathbf{C} \times \mathbf{M}, \quad (5)$$

where \mathbf{B} is the mean prey density of 20 individuals m^{-3} (Jenkins and Keeley, 2010), \mathbf{C} is a fish foraging area of 1.06 m^2 (Hughes et al., 2003) and \mathbf{M} is flow velocity in $cm\ s^{-1}$. We assume that consumption capacity of the fish was proportional to its own mass (5% daily; Boujard and Medale, 1994) and the mass of prey was defined as (Smock, 1980):

$$\text{Mass} = \exp^{-5.021+2.88\ln(\mathbf{D})}. \quad (6)$$

For a given prey density, we used a more realistic non-uniform prey size distribution [0–2 mm (51%), 2–4 mm (43%), 4–6 mm (5%), 6–8 mm (0.9%) and 8–10 mm (0.1%)] in diameter as measured *in situ* in typical trout streams (Guensch et al., 2001).

Because in nature fish do not feed continuously throughout the day, we then sought to identify an optimum strategy when feeding and locomotor behaviors were combined. To do this, we divided a 24 h day into halves (12 h each), roughly corresponding to night and day, and assumed that fish forage exclusively during the day. This allowed us to include three foraging scenarios in our model: (1) foraging while refuging; (2) foraging while freestream swimming; and (3) refuging without foraging at night and foraging in the freestream during daytime (hereafter defined as a 'combined' strategy). Based on Charnov's (1976) diet model, we assume that fish preferentially consume larger prey whenever available. Note that our approach does not take into account behaviors such as group hierarchy or predator avoidance and territoriality.

Finally, to translate model results of energetic gain to a value with biological meaning, we calculated a relative maximum benefit as:

$$E_{Net}/E_{Locomotion}. \quad (7)$$

In this case, 100% relative maximum benefit indicates that a particular foraging strategy used for one day can result in one extra day of surplus energy before more food must be acquired, thereby designating energy available for other critical activities (e.g. migrating, growth, reproduction). Consequently, relative benefit provides an indication of the long-term benefit of adopting a particular feeding strategy in a way that reporting oxygen consumption units does not.

Table 1. Overview of model factors and description, data values and sources

Cost–benefit factors	Definition	Value or method of computation	Source
A Prey size distribution	Natural size distribution of invertebrate drift measured <i>in situ</i> in typical trout streams. Recorded as a proportion of whole size (%) and as diameter (mm) [see D]	0–2 mm, 51.0% 2–4 mm, 43.0% 4–6 mm, 5.0% 6–8 mm, 0.9% 8–10 mm, 0.1%	Hughes and Dill, 1990 Guensch et al., 2001 Hughes et al., 2003
B Prey density	No. of prey individuals per m ³ in a typical trout stream	0–20 individuals m ⁻³	LaPerriere, 1981, 1983 Hughes and Dill, 1990 Guensch et al., 2001 Jenkins and Keeley, 2010
C Foraging area	Total area around an individual fish where it will attack prey	1.06 m ²	Hughes et al., 2003
D Diet size composition	Diameter (D in Eqn 4) of prey preferentially consumed	2–10 mm	Hill and Grossman, 1993 Braaten et al., 1997 Nakano et al., 1999 Guensch et al., 2001 Hughes et al., 2003
E Relative daily food intake	Maximum total daily food intake relative to body size of trout (%)	3.8–5.0%	Brett and Groves, 1979 Boujard and Medale, 1994 Nakano et al., 1999
F Daily feeding hours	No. of hours spent feeding each day by a visual predator such as trout	Daytime: constant feeding (12 h) Night time: resting	Hughes and Dill, 1990 Hill and Grossman, 1993 Braaten et al., 1997
G Prey capture time	Time required to capture a prey, including initiation of prey approach, prey intercept and return to starting location (in s)	2–20 s	Bachman, 1984 Puckett and Dill, 1984 Bannon and Ringler, 1986 Hughes and Kelly, 1996 Jenkins and Keeley, 2010 Watz and Piccolo, 2011 Hughes and Kelly, 1996 Hughes et al., 2003
H Attack rate	Typical no. of preys attacked per hour	0–300	Elliott and Davison, 1975
I Energy conversion	Conversion of oxygen consumption in mg O ₂ kg ⁻¹ h ⁻¹ to joules (J)	1.00 mg O ₂ =13.56 J	Elliott, 1976
J Prey assimilation efficiency	Energy assimilated of typical invertebrate prey after accounting for digestion and excretion. Taken as the constant 0.68 (Hill and Grossman, 1993)	58–72%	Brett and Groves, 1979 Ware, 1982 Hill and Grossman, 1993 Rosenfeld and Boss, 2001 Jenkins and Keeley, 2010
K Prey mass	Mass (mg) of each prey relative to size (diameter D , mm)	$\exp(-5.021+2.88 \ln(\mathbf{D}))$	Smock, 1980
L Prey energy content (E_{Prey})	Total energy (in J) of each prey item relative to size (diameter D , mm)	$0.3818 \times \mathbf{D}^{2.46}$	Jenkins and Keeley, 2010
M Flow velocity	Flow velocities typically encountered in streams	0–100 cm s ⁻¹	Hughes and Dill, 1990 Gido et al., 2000 Guensch et al., 2001 Enders et al., 2005 Hayes et al., 2007 Jenkins and Keeley, 2010 Urabe et al., 2011
N Flow reference velocity	Flow velocity used for measuring the cost of prey attack [see R]	68 cm s ⁻¹	This study
O Predator mass	Mass of drift-feeding predatory fish	500 g	Robins and Ray, 1986

RESULTS

Cost of swimming

Oxygen consumption increased with swimming speed for both refuging and freestream swimming fish. However, refuging fish did not increase their oxygen consumption until they swam faster than 68 cm s⁻¹ ($y=66.6+0.30 \times 1.07^x$, where y is oxygen consumption and x is swimming speed, repeated measures ANOVA, $F_{1,126}=72.9$, $P<0.01$). By comparison, fish in the freestream showed significantly greater oxygen consumption at each incremental swimming speed ($y=47.30+17.79 \times 1.03^x$; Fig. 1).

Cost of prey attack

Oxygen consumption during prey attacks increased more quickly for refuging than for freestream swimming individuals (regression $P \leq 0.0001$), indicating that the cost of each attack was greater for

refuging trout (mean±s.e.m., 1.28 ± 0.18 mg O₂ kg⁻¹) than for trout in the freestream flow (0.78 ± 0.20 mg O₂ kg⁻¹; Fig. 2). For example, at a routine swimming speed of 68 cm s⁻¹, foraging in the freestream was 40% less costly compared with foraging while refuging (ANCOVA, $F_{1,31}=126.6$, $P<0.01$). This was speed dependent, for at a lower swimming speed of 10 cm s⁻¹, this difference reduced to 6%.

Prey detection

Refuging and freestream swimming trout made the same number of attacks on prey (two-way ANOVA, refuge $F_{4,58}=1.03$, $P=0.32$; freestream $F_{1,58}=0.72$, $P=0.58$), indicating that the cylinder did not obscure prey detection for refuging trout. The proportion of prey attacked decreased as flow velocity increased for both behaviors ($F_{4,58}=21.05$, $P<0.01$; Fig. 3A).

Table 2. Model factors, formulae and data sources

Cost–benefit factor	Formulae	Source
P Cost of swimming ($E_{Locomotion}$ in $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$)	$y_{refuge}=66.60+0.30 \times (1.07^M)$ $y_{freestream}=47.30+17.79 \times (1.03^M)$	Empirical data from this study
Q Prey capture success ($P_{Capture}$)	$y_{refuge}=1/(1+\exp^{-(M-58.811)/-10.579})$ $y_{freestream}=1/(1+\exp^{-(M-86.383)/-16.515})$	
R Cost of each prey attack (E_{Attack} in $\text{mg O}_2 \text{ kg}^{-1} \text{ attack}^{-1}$) at flow reference velocity of 68 cm s^{-1}	Refuge= 1.28 ± 0.18 Freestream= 0.78 ± 0.20	Derived data
S No. of prey available per hour	Prey size distribution \times prey density \times foraging area \times flow velocity [i.e. $\mathbf{A} \times \mathbf{B} \times \mathbf{C} \times \mathbf{M}$]	
T Maximum food intake per hour	Relative daily food intake \times predator mass/daily feeding hours [i.e. $\mathbf{E} \times \mathbf{O} / \mathbf{F}$]	Main model
U No. of attacks per hour	Defined as the lowest value of the following parameters: (a) prey captures per hour [i.e. $3600/\mathbf{G}$] (b) no. of prey available per hour [see S] (c) max. prey intake per hour [i.e. \mathbf{T}/\mathbf{K}]	
W Cost of attacks per hour ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$)	Cost of each prey attack \times no. of attacks per hour \times flow velocity/flow reference velocity [i.e. $\mathbf{R} \times \mathbf{S} \times \mathbf{M} / \mathbf{N}$]	
X Total energy cost per hour (E_{Cost})	Cost of swimming per hour + cost of attacks per hour [i.e. $\mathbf{P} + \mathbf{W}$]	
Y Total energy intake per hour (E_{Gain})	No. of attacks per hour \times prey capture success \times prey energy content \times prey assimilation efficiency [i.e. $\mathbf{U} \times \mathbf{Q} \times \mathbf{L} \times \mathbf{J}$]	
Z Net energy gain per hour (E_{Net})	$E_{Gain} - E_{Cost}$ [i.e. $\mathbf{Y} - \mathbf{X}$]	

Prey capture success

Prey capture success was lower for refuging individuals than for swimming fish in the freestream (two-way ANOVA, $F_{1,63}=28.2$, $P<0.01$). This was most evident at the highest flow velocities ($\geq 51 \text{ cm s}^{-1}$). The success of both feeding strategies decreased with increasing flow velocity ($F_{4,63}=45.8$, $P<0.01$). For a given success percentage, individuals in the freestream can inhabit faster flow environments than refuging individuals (Fig. 3B; Table S1).

Data-driven cost-benefit model outcome

Fig. 4A shows the net energetic benefit for trout feeding continuously either while refuging or in freestream flow. At flows $<25 \text{ cm s}^{-1}$, the two foraging strategies were energetically identical. When flow velocity exceeded 25 cm s^{-1} , it was more energetically favorable for trout to feed in freestream flow. The model-predicted

best 24 h strategy was to combine freestream feeding and refuge swimming, where fish feed in freestream flow for 12 h and then refuge (without feeding) for 12 h (i.e. ‘combined’ strategy; Fig. 4A).

Under average conditions, refuging trout swimming at 25 cm s^{-1} can acquire enough energy in a single day to last an additional ~ 1.4 days (140%). This value was ~ 1.2 days for fish foraging in the freestream and ~ 1.5 days for trout adopting the combined strategy defined above (Fig. 4B).

We found that optimal feeding behavior depends on the magnitude of the flow velocity. For flows less than 50 cm s^{-1} , refuging provides a greater relative energetic benefit than freestream swimming. For flows greater than 50 cm s^{-1} , the benefit of refuging disappears and it is better to forage continuously in the freestream. However, the best overall strategy is to forage half the time in freestream flow and to refuge without feeding for the remaining time

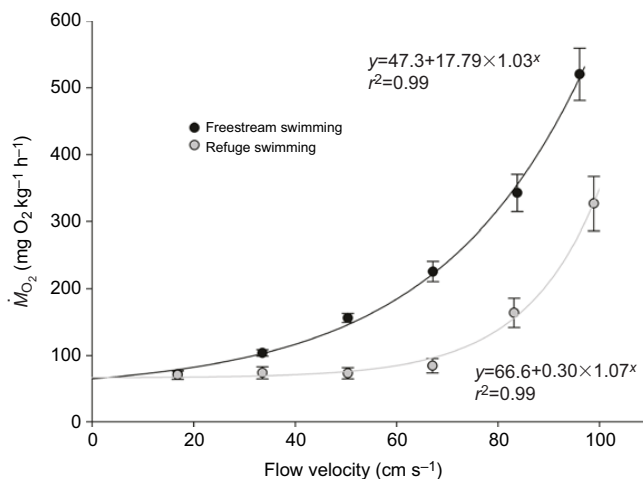


Fig. 1. Energetic costs of swimming and refuging. Rate of oxygen consumption (\dot{M}_{O_2}) of rainbow trout swimming in freestream flow versus refuging behind a 5 cm diameter cylinder. As flow velocity increases, the cost of swimming in the freestream increases more quickly compared with that when refuging behind a cylinder. The cost of refuging is similar across flow velocities until flow exceeds 68 cm s^{-1} . Data are means \pm s.e.m.

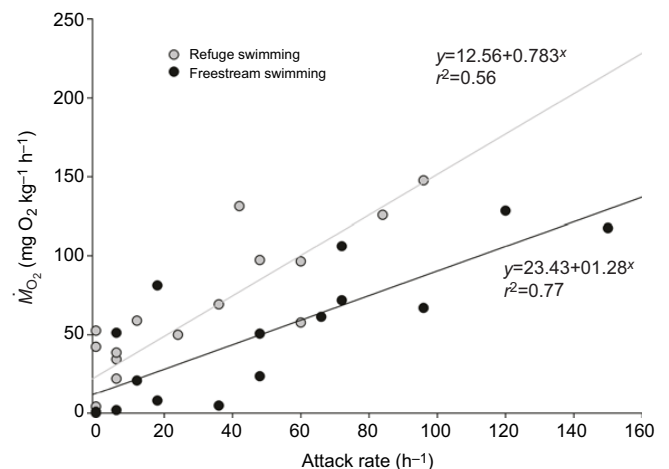


Fig. 2. Energetic costs of attacking prey in flow. At a chosen flow velocity of 68 cm s^{-1} , rate of oxygen consumption (\dot{M}_{O_2}) of trout feeding on drifting prey increases linearly with attack rate during both freestream swimming and refuging. The slopes of the regression lines depict the energetic cost associated with each individual prey attack. The cost of attack is 64% greater during refuging compared with freestream swimming, reflecting the higher cost required to transition across a velocity gradient from refuging in a vortex street to intercepting prey in the freestream flow.

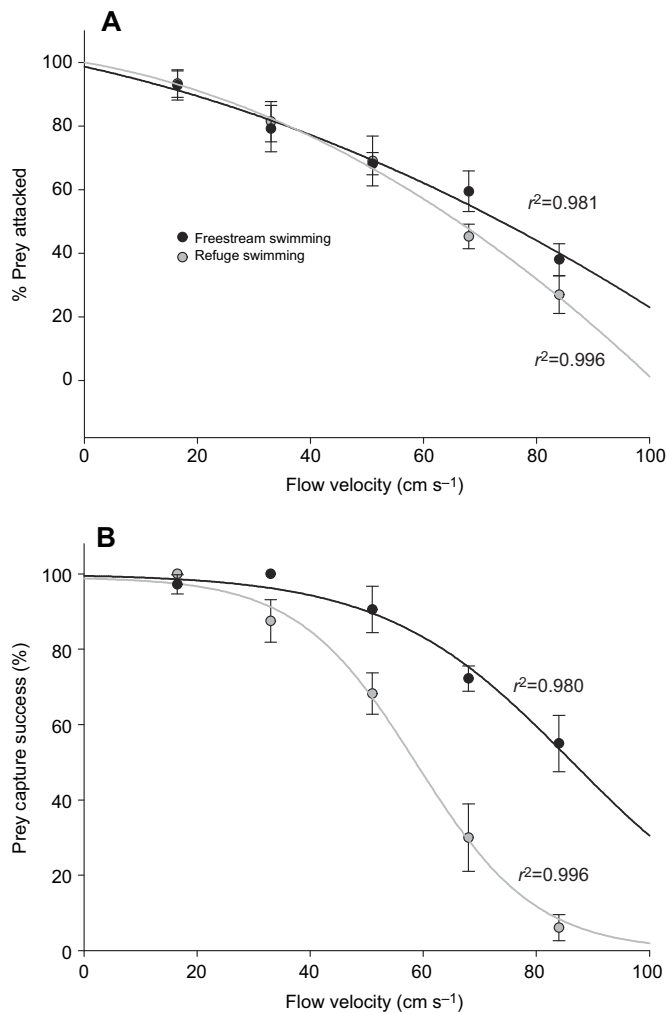


Fig. 3. Attack rate and capture success for drift-feeding trout across flow velocities. (A) The percentage of prey attacked by trout swimming in the freestream versus refuging is not significantly different. In low flows (<68 cm s⁻¹), trout attack prey the majority of the time regardless of refuging behavior, while at higher flows (≥68 cm s⁻¹), attack rate is comparatively lower in refuging trout. (B) As flow velocity increases, prey capture success decreases for both behaviors, but more substantially for refuging trout. Data are means ± s.e.m.

(combined strategy; Fig. 4). This strategy greatly expands the range of flow velocities where fish can maintain an energetic surplus, up to 75 cm s⁻¹ in our model (Fig. 4B).

Prey size and density requirement

To compensate for the increasing energetic costs of foraging, trout must feed on increasingly larger and more abundant prey as flow velocity increases (Fig. 5; Fig. S1). Prey size and density requirements increase faster with flow velocity for refuge-feeding individuals than for freestream-feeding individuals. As a result, refuging individuals would in theory require 8 mm long prey when swimming at 70 cm s⁻¹ whereas freestream individuals would only need these prey sizes when swimming at 90 cm s⁻¹ (Fig. 5A). Similarly, refuging individuals require densities of at least 15 prey m⁻³ of water volume in a flow of 60 cm s⁻¹, whereas freestream individuals only need a density of 3 prey m⁻³ of water volume at the same flow velocity (Fig. S1). When fish combine refuging and freestream swimming behaviors, their locomotion costs are minimal, which allows them to eat smaller and fewer prey

than if they were exclusively refuging or swimming in freestream flow (Fig. 5B) and occupy flows with fewer prey (Fig. S1). Regardless of foraging strategy, our model predicts that trout need to feed on prey larger than 2 mm, at density patches of at least 2 prey m⁻³, and conduct a minimum of 20 attacks per hour in order to obtain enough energy to sustain foraging costs (Fig. 5).

DISCUSSION

Understanding what drives species distributions in nature is one of the fundamental goals of ecology. The energetics of feeding and locomotion are widely acknowledged to play a major role in influencing the distribution, abundance and behavior of organisms, but direct measurements of their costs are often lacking (Hughes and Kelly, 1996; Grossman, 2014; Piccolo et al., 2014). In many aquatic ecosystems, fish preferentially occupy high flow habitats (Guensch et al., 2001; Fulton and Bellwood, 2005; Grossman, 2014; Johansen, 2014; Piccolo et al., 2014), despite the high associated costs of locomotion (Fulton et al., 2013). It has long been assumed that fish in high flows should seek to exploit refuges to reduce foraging costs (Liao et al., 2003a; Johansen et al., 2007, 2008; Taguchi and Liao, 2011; Piccolo et al., 2014; Rosenfeld et al., 2014). However, our empirical cost-benefit model challenges this assumption by showing the opposite: in high flow, it is most energetically favorable for fish to either (1) refuge without foraging or (2) forage in the freestream without refuging. These results are primarily due to the cost of each attack relative to attack success rate, and may help to explain why trout often forage heavily in relatively open, freestream sections of rivers during an insect hatch (Grossman and Boulé, 1991). At the highest flow velocity tested (100 cm s⁻¹), we found that all foraging strategies failed, even though trout both in our experiments (Fig. 1) and in nature (Cocherell et al., 2011) are physically capable of swimming at these speeds and beyond. This is because once foraging costs are considered, swimming at these speeds is not energetically favorable, which may explain why fish are not typically found in such high flows in nature, and will vacate habitats once flow velocity exceeds a certain level (Gido et al., 2000; Cocherell et al., 2011).

The capacity to exploit refuges to save locomotor energy has frequently been used to explain fish distributions in high flow habitats such as rivers and exposed coral reefs, where access and monitoring may be difficult (Hughes and Dill, 1990; Liao et al., 2003a; Johansen et al., 2007, 2008; Urabe et al., 2011; Taguchi and Liao, 2011). This study confirmed this capacity in trout, revealing an almost 50% reduction in swimming costs at high speeds (>65 cm s⁻¹). However, we also observed a large (~65%) and unexpected increase in the cost of attacking prey in the freestream while refuging, presumably as a result of the high cost of traversing a strong velocity gradient when leaving a vortex street refuge (Liao et al., 2003b). Such a significant increase in energy usage for feeding has previously only been theorized (Puckett and Dill, 1984; Boisclair and Tang, 1993; Hughes and Kelly, 1996; Guensch et al., 2001; Rosenfeld and Boss, 2001; Jenkins and Keeley, 2010). The energetics of foraging have been identified as one of the important drivers of animal movement (Pyke, 1984). Here, we directly reveal the mechanism underlying the substantial increase in energy use during foraging for the first time in drift-feeding fishes.

Fish should seek to minimize the combined cost of metabolic maintenance, swimming and prey attack relative to the energetic gains from each attack. The optimal strategy likely depends on flow velocity and available prey size. By including our data on the energetic cost of attack into the total daily energy budget, we can derive the specific range of conditions under which it may be more

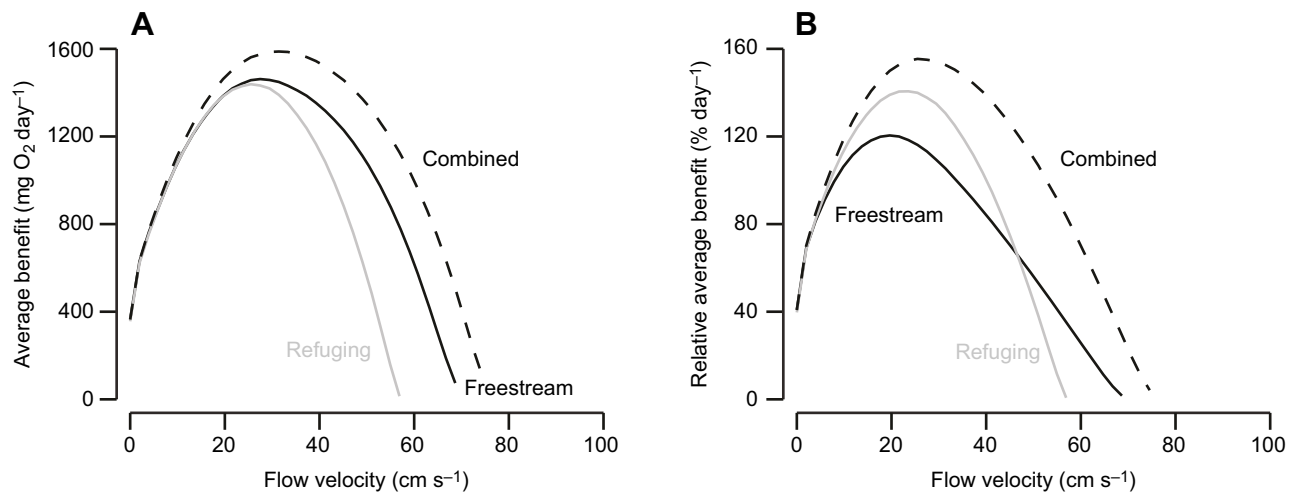


Fig. 4. Model of the average absolute and relative energetic benefits of different feeding strategies in flow. (A) For flow velocities of $<25 \text{ cm s}^{-1}$, the absolute benefit (defined as the energetic gain from food acquisition minus the cost of acquisition) of foraging exclusively either in freestream flow or behind a refuge is similar. At flow velocities of $25\text{--}70 \text{ cm s}^{-1}$, it is energetically more beneficial to forage in the freestream flow versus refuging. (B) By dividing the absolute benefit by the cost of locomotion, the relative benefit of each foraging strategy can be assessed (a value of 100% is defined as a full day of surplus energy). At flows of $10\text{--}50 \text{ cm s}^{-1}$, foraging while refuging provides the greatest relative benefit because of the low difference in swimming cost between the refuge and the freestream. At swimming speeds greater than 50 cm s^{-1} , however, foraging in the freestream is the energetically most advantageous strategy because the lower cost of foraging in the freestream outweighs the added cost of attack from a refuge. The highest energetic benefit over a 24 h period is realized by refuging without feeding for 12 h and foraging in the freestream for 12 h at all flow velocities $>20 \text{ cm s}^{-1}$ (dashed line). This combined strategy also enables an energetic benefit to be gained from a greater range of flow velocities than possible for either behavior alone (up to 75 cm s^{-1}).

energetically beneficial to exploit or avoid a flow refuge. Previous studies indicate that fish interact with flow refuges using at least three different strategies: (1) reside in a refuge and only enter the freestream during an attack, (2) reside and forage in the freestream, or (3) forage in the freestream and seek refuge when not foraging (Hill, 1989; Grossman and Boulé, 1991; Guensch et al., 2001; Piccolo et al., 2014). When we used our data-driven model to explore these three strategies, we found that there is an optimum range of flow velocities (within approximately $10\text{--}50 \text{ cm s}^{-1}$; Fig. 4) that provides the greatest energetic benefit to trout. It is perhaps not surprising that this velocity range is equivalent to the natural conditions that are typically observed for rivers that contain the greatest abundance of trout (Hill and Grossman, 1993; Guensch et al., 2001; Urabe et al., 2011).

Why, in low flow environments, is foraging while refuging better than foraging in the freestream flow? We show that when trout forage in currents less than 50 cm s^{-1} , they can on average acquire 1.4 times their daily energy requirements (and even higher under optimal conditions). This energy surplus is possible because of the low cost of locomotion behind the refuge. In addition, slower currents lead to a reduced velocity gradient between the refuge and the freestream flow, which minimizes the cost of exiting the vortex street to attack prey. The lower cost of attack and higher attack success rate in slower currents allows trout to acquire surplus energy, which can then be used for growth, maintenance and reproduction. It is worth noting, however, that the data presented here are specific to passively drifting prey. Slower current may allow active prey to execute evasive maneuvers if their sensory systems are not disturbed by the turbulent flow (e.g. Johansen and Jones, 2013).

In high flow habitats ($>50 \text{ cm s}^{-1}$), however, the benefit of refuging disappears when trout forage on passively drifting prey. We found that refuging trout suffered a net energetic loss due to a 65% increase in the cost of attacking prey and a 40% reduction in attack success rate, demonstrating that it is more costly to forage from a refuge than from freestream flow. Specifically, the energetic

benefit of refuging while foraging is inversely related to flow velocity. We suggest that this is because the energy needed to accelerate from a place of refuge into faster freestream flow necessitates traversing across a steep velocity gradient. Compared with foraging in freestream flows, refuging fish that dart out to capture food are expected to accelerate more quickly in order to overcome these velocity gradients. The large amplitude kinematics of fast accelerations is significantly different from that of steady swimming (Akanyeti et al., 2017), and typically relies on anaerobic rather than aerobic energy production (Viedeler and Weihs, 1982; Reidy et al., 2000). This is likely the main contributor to the high energetic requirements of this behavior, which leads to an inability of feeding trout to maintain an energy surplus while refuging because the cost of each attack is greater than energy content of the prey. Importantly, our methods did not explicitly measure anaerobic energy consumption during attacks but the combined anaerobic and aerobic costs, based on the assumption that anaerobic metabolite build-up from each $<1 \text{ s}$ anaerobic component of attack was also repaid during each of the 10 min measurement periods. Specifically, depending on the number of attacks, the measurement period encompassed no less than 30–600 times longer aerobic activity than anaerobic activity, which is substantially longer than previously recorded recovery periods in trout (Wieser et al., 1985).

Contrary to prevailing theory, our model predicts that individuals living in flows $>50 \text{ cm s}^{-1}$ should completely avoid refuges while foraging. This counterintuitive insight is only possible because we employ the first direct measurements of feeding costs in controlled conditions. Our results are consistent with field observations of wild trout foraging predominantly in the freestream (Grossman and Boulé, 1991) and avoiding the fastest flowing sections of rivers (Hill and Grossman, 1993). At the highest flow velocities in our study ($>81 \text{ cm s}^{-1}$), trout can only ensure adequate energy intake by foraging in the freestream when prey densities are greater than $15 \text{ individuals m}^{-3}$ (Fig. S1). This suggests that trout in rivers will

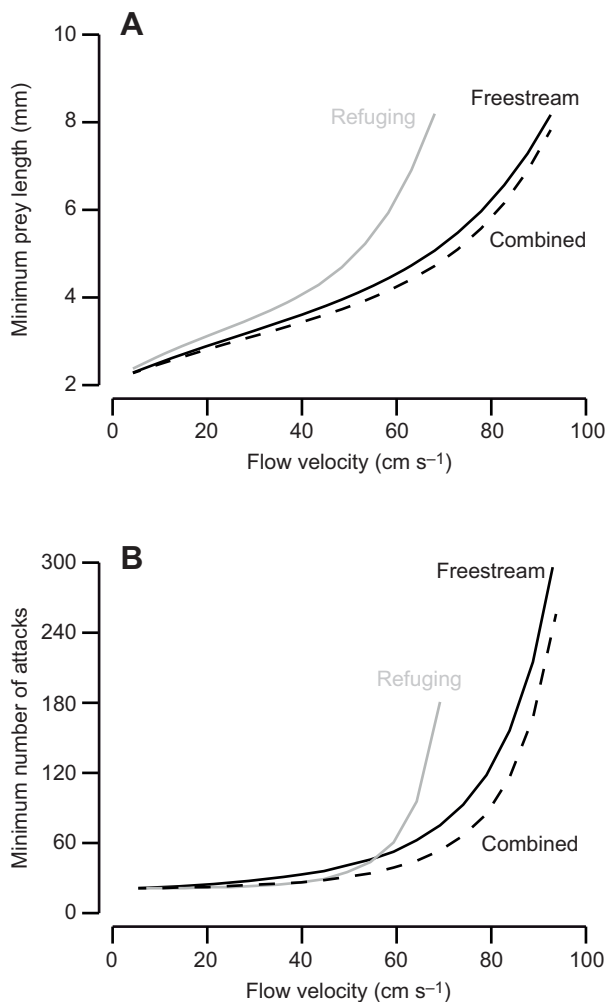


Fig. 5. Model of the preferred prey size for drift-feeding trout at a given flow velocity and the minimum number of attacks required to provide an energetic surplus. (A) Taking into account the caloric content of the prey, the cost of locomotion and attack while refuging behind a cylinder or swimming in the freestream, and the likelihood of prey capture, trout should not target prey less than 2 mm in length. Relative to free swimming at a given flow velocity, trout that are solely refuging behind a cylinder need to capture larger, higher caloric content prey because of the added attack costs originating from a refuge and reduced likelihood of capture. (B) Minimum number of attacks on prey required for a locomotion strategy to be energetically favorable. Minimum attack numbers at each flow velocity are defined as the lowest value of the following parameters: maximal successful prey captures per hour, number of prey available per hour, and maximum food intake per hour based on prey size availability. A foraging strategy consisting of feeding in the freestream and refuging while not feeding (dashed line) allows trout to minimize the number of prey attacks across all flow velocities above 50 cm s⁻¹.

not occupy regions of freestream flow during periods of low prey density. Although our results do not take into account the potential benefit of a surprise attack on an unsuspecting prey, they do highlight the importance of considering the relatively high cost of foraging when refuging, which has been absent in previous energetic models (see Piccolo et al., 2014, for review). Perhaps most importantly for fisheries conservation managers, we argue that a classification of optimum habitat conditions cannot be determined solely on the basis of swimming energetics. Our data suggest that preferred flow velocities in the field are limited not only by swimming capacity but also by the energetic demands of foraging. This observation may also help explain potential discrepancies

between predicted and realized habitat and movement patterns in the wild (Piccolo et al., 2014).

Our results lead us to suggest that the main benefit of feeding from a refuge may not be to save on locomotion costs (which occurs only at lower flow velocities) but as a strategy for resilience to unpredictable food conditions. Temporal fluctuations in food availability are common in nature (Nakano et al., 1999; Hamner et al., 2007; Jenkins and Keeley, 2010; Armstrong and Schindler, 2011). In unpredictable habitats, individuals that occupy flow refuges will require less energy over time and will be more resilient to prolonged periods of low food availability. Such refuging patterns have been observed in rivers that experience frequent periods of low prey abundance (Hughes and Dill, 1990) and pulses of high current (Cocherell et al., 2011). Within an optimal range of flow velocities (here 10–50 cm s⁻¹), refuging individuals also require prey that are less calorie rich to sustain the same energetic benefits as individuals swimming in freestream flow. This allows refuging individuals to forage on a wider variety of prey that may be smaller and have less caloric content, while gaining greater resilience to agonistic interactions associated with, for example, competition for food (Armstrong and Schindler, 2011) or differential capture success rate for smaller versus larger sized trout (a potential caveat not examined in this study).

As flow velocity increases, the cost of swimming and foraging also increases while the ability to detect and capture prey decreases (Hill and Grossman, 1993; Braaten et al., 1997). Trout may deal with this problem by only targeting larger, calorie-rich prey in order to compensate for the diminished opportunities to capture prey. In nature, invertebrate prey of 8 mm or greater make up less than 1% of all drifting food (Table 1), yet trout preferentially select these larger prey (Nakano et al., 1999). It must be noted, however, that faster flows generally deliver more and larger prey over a unit of time (Hill and Grossman, 1993; Hayes et al., 2007; Jenkins and Keeley, 2010). Based on prey size distribution and caloric prey content in natural rivers, our energetic model predicts the preferred prey size of foraging trout under different feeding strategies and flow velocities. We predict that refuging trout occupying habitats with flows greater than 65 cm s⁻¹ should solely select prey of 8 mm or greater in order to account for the costs of foraging. The need to target large prey based on energetics may explain why trout have been observed to leave sections of rivers that appear to contain abundant but small prey (Hughes and Dill, 1990; Gido et al., 2000). Likewise, drift-feeding trout in fast flows appear to avoid small prey even when their abundance is greater by several orders of magnitude than larger prey (Hill and Grossman, 1993; Nakano et al., 1999).

Our work suggests that, regardless of flow velocity, the minimum prey size that trout should eat must be 2 mm long in order to provide enough energy (equivalent to ~2.1 J) to cover the energetic cost of a successful capture (Fig. 5). The majority of invertebrate prey found in rivers range from 0.1–10.0 mm in length, with more than 50% of all prey being 2.0 mm or less (Table 1). Therefore, it may not be energetically favorable for trout to forage on the majority of available prey. Indeed, examination of stomach contents has revealed that trout preferentially forage on prey greater than 2.0 mm in length (Hill and Grossman, 1993; Braaten et al., 1997; Nakano et al., 1999; Guensch et al., 2001; Hughes et al., 2003). This discrepancy between prey size availability and stomach content analyses has previously been attributed to large gill raker spacing, which may not be effective for filtering and retaining smaller prey (Bisson, 1978; Hughes et al., 2003). We do not believe this to be the case, given that trout are not filter feeders but target and capture individual prey. In addition, true filter-feeding fishes can capture

prey much smaller than their gill raker spacing because of a unique vortex filtration mechanism (Motta et al., 2010; Paig-Tran et al., 2013). It is not known whether trout possess such a filtration mechanism. Here, we provide an alternative explanation based on energetics. Fishes foraging on individual prey in flow such as trout and certain coral reef fishes should consider the energy content of each prey, which over time must be greater than the cost of its acquisition. To our knowledge, this is the first direct experimental demonstration that supports an energetics argument to explain such selective foraging patterns in fishes.

Values of foraging costs in flow should be considered for cost–benefit models, along with consideration of prey detection and capture abilities, in order to improve their accuracy from existing models in which these parameters are lacking (Hughes and Dill, 1990; Hughes and Kelly, 1996; Guensch et al., 2001; Hughes et al., 2003; Urabe et al., 2011; Piccolo et al., 2014). We account for these parameters here, leading us to believe that our general approach can be broadly applied to both freshwater and marine species, though the details of prey size, capture success and energetic costs may differ. The utility of our approach is that it predicts energetically favorable flow velocities for fish (herein described as optimum flow range). As such, it provides a mechanistic basis for understanding why individuals in nature are typically found associating with refuges only within a specific range of flow velocities. This approach, where links between energetic demand and habitat usage are demonstrated, is starting to illuminate our understanding of distribution patterns in a variety of species (Urabe et al., 2011; Rosenfeld et al., 2014). The ability to determine *a priori* the optimum flow requirements will help us better predict movement and habitat usage patterns not only for salmonids in rivers but also for other ecologically and commercially important species (e.g. Kiflawi and Genin, 1997; Zeller, 2002; Johansen et al., 2014, 2015). As such, we believe that our model has strong conservation implications that can be applied broadly.

By using respirometry to directly measure foraging costs in the lab, our empirical approach provides critical new insight that challenges established assumptions of ecology and behavior in current-swept ecosystems. We demonstrate that in high flow habitats, hydrodynamic refuges are not energetically favorable locations, and that the best feeding strategy across flow velocities is adaptive: refuging in slower flows when not foraging and only foraging in faster freestream flows. Our experimental results provide a framework to understand the mechanisms underlying habitat preferences and movement patterns in current-swept environments, and generates hypotheses that can be tested to see how well these strategies are employed by fish in nature.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: J.L.J., J.C.L.; Methodology: J.L.J., J.C.L.; Software: O.A., J.C.L.; Validation: O.A.; Formal analysis: J.L.J., O.A.; Investigation: J.L.J., J.C.L.; Resources: J.C.L.; Data curation: J.L.J., J.C.L.; Writing - original draft: J.L.J.; Writing - review & editing: J.L.J., O.A., J.C.L.; Supervision: J.C.L.; Project administration: J.C.L.; Funding acquisition: J.C.L.

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Supplementary information

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