Efficiency is not always the name of the game: Pile perch prefer to swim slower than their optimal speed

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Introduction

The efficient and effective use of movement is essential for survival in mobile animal species. Among a plethora of other uses, movement is used to locate food, find mates, explore the environment, defend territories, and avoid danger (Pyke 1978, Gilroy and Lockwood 2012, Fortin et al. 2005, Rosell et al. 1998, Teyke 1989). The physiological and morphological parameters determining movement, and how different aspects of movement may be measured, are therefore significant areas of interest for animal biologists. In addition, knowledge of the movement of animals allows improvement of welfare and growth conditions in captive animals, and facilitates the study of other behaviours in both wild and captive settings.

While animals move at a wide range of speeds in natural environments, it has been experimentally established that each individual has a speed at which their energy use is most efficient, after accounting for body mass and distance travelled (Wilson et al. 2015, Tucker 1970). This is their optimal speed, or U_{opt} (Weihs 1973, Pyke 1981). U_{opt} depends on metabolic rate, body size and shape, and likely other morphological and physiological parameters. U_{opt} therefore varies among species according to habitat and life history strategy (Weihs 1973, Tudorache et al. 2008, Wakeman and Wohlschlag 1982, Ware 1978). In temperate fish species, U_{opt} may vary from as low as 1 to as high as 5 body lengths per second (bl s^{-1}) (Palstra et al., 2020; Tudorache et al., 2008; Tudorache et al., 2011).

While U_{opt} may represent the most efficient speed of motion for an individual, the actual speed at which animals move is volitional and therefore linked to various other factors. Individual energetic needs, while determining physical parameters like U_{opt}, also contribute to behavioural factors such as individual "personality" traits. Individuals with greater metabolic rates may display greater tendency to exploratory behaviour (Fu et al. 2021, Binder et al. 2016), and therefore demonstrate a greater preferred swimming speed, or U_{pref}, than would be predicted by their U_{opt}. Habitat and life history strategy may also contribute to U_{pref}. Fishes found in complex habitats may tend to swim more slowly than their U_{opt}, in order to avoid obstacles (Priyadarshana et al., 2001). Fishes with hunting strategies such as "sit-and-wait" predators may spend the majority of their time completely immobile (Armstrong, 1986; Tolley & Torres, 2002). However, in pelagic and generalist fish species that spend the majority of their time moving it may be that U_{pref} is predicted by U_{opt}. In the brook trout *Salvelinus fontinalis*, a pelagic migratory species, U_{pref} strongly resembles U_{opt} at speeds greater than 25 cm s^{-1}, or around 1 bl s^{-1} (Tudorache et al., 2011).

The social environment may also determine the extent to which individual U_{opt} determines U_{pref}. Individuals of social species will alter preference for abiotic parameters such as temperature in order to spend time with conspecifics (Cooper et al., 2018; Nay et al., 2021), however whether the presence of a conspecific disrupts the relationship between U_{opt} and U_{pref} remains unclear. As different individuals are likely to have different U_{opt} and U_{pref} values, determining whether a fish will sacrifice social interaction to swim at their preferred speed or will sacrifice swimming speed in favour of social interaction is a key consideration for social species (Jolles et al., 2017).

Coincidence of U_{opt} and U_{pref} has been previously studied in one species, *S. fontinalis*, in the context of determining whether U_{opt} or U_{pref} may represent a better indicator of the best swimming speed to facilitate growth in aquaculture tanks (Tudorache et al., 2011). U_{opt} was found to be a good indicator of U_{pref}, likely relating to this species' migratory lifestyle. When travelling long distances with limited feeding opportunities is a key aspect of a species' ecology, sustained swimming near U_{opt} is likely an energetically favourable strategy. Natural selection may then favour individuals whose U_{pref} coincides with their U_{opt}. However, whether this relationship holds in non-migratory species is yet to be determined.

Our study aims to build on this work by investigating the relationship between U_{opt} and U_{pref} in a marine generalist species, the pile perch *Rhacochilus vacca*. In addition, we aimed to investigate how the relationship between U_{opt} and U_{pref} may differ when this social species (Munsch et al. 2016) is alone versus in the presence of a conspecific. We predicted that U_{opt} would be positively correlated with U_{pref}, though this relationship may be less strong in *R. vacca* as a marine generalist compared with previous studies on the migratory *S. fontinalis*. We also predicted that as a social species, *R. vacca* would alter U_{pref} when swimming in pairs in order to remain with a conspecific.

Methods

1. Study animals

Pile perch were collected between 18/07/2023 and 13/08/2023 from Jackson Beach, San Juan Island, WA, USA (48.51995, -123.01105). Fish were caught by seine netting from the shore. Following species identification, fish were weighed and those weighing over 30g were selected for use in our study. Smaller fish were not used due to error associated with conducting respirometry on small fishes given the size of our swim tunnel. Fish were maintained in a tank (130 × 60 × 15 cm, filled with seawater to a depth of 9 cm) with a constant in- and out-flow of seawater at ambient temperature (~14°C). Fish were kept in the lab for at least two days prior to beginning data collection. Prior to respirometry, morphological measurements (total length, body depth, body width) were collected to account for the solid blocking effect of each fish on swim tunnel flow speed. Data were collected for a total of 16 fish, allowing 16 respirometry trials as well as 16 individual and seven paired swimming trials. Data were collected from 02/08/2023 - 16/08/2023. In order to validate our methods, two pilot fish were also run between 31/07/2023 - 02/08/2023.

2. Respirometry

Fish were placed in a Steffensen-type 8.5 l swim tunnel respirometer with a cross-sectional area of 99 cm^2 (Figure 1). Swim tunnel flow rate was calibrated using a Höntzsch flowmeter and SEW Eurodrive voltmeter. Temperature was maintained at a constant 14°C using a thermometer and Thermofischer cooler, setpoint 14°C with a hysteresis of 0.1°C. Oxygen saturation was measured using a Fibox 3 oxygen metre. Intermittent flow respirometry was carried out in cycles of 10min, with a 270 second flush period, 30 second wait period, and a 300 second measurement period. Fish were acclimated in the swim tunnel for 6-12 hours at a constant swim speed of 0.5 body lengths per second (bl s^{-1}). Respirometry data was collected using the software Autoresp (Logigo systems, Denmark). Following acclimation, swim tunnel speed was increased by increments of 0.5 bl s^{-1} every 30 minutes. For each speed increment, the fish was recorded with a Logitech camera for a minimum of 30 seconds to capture pectoral fin beat frequency at each swim speed. The camera was mounted approximately 40 cm above the tank and a mirror was placed at a 45° angle at the side of the tank to simultaneously record dorsal and lateral views of the fish. Speed increase continued until the fish reached its critical swimming speed (U_{crit}), defined as the point at which swimming ceased and the fish rested against the back grill of the swim tunnel for at least five consecutive seconds. At this point, the flow rate was decreased back to 0.5 bl s^{-1} and oxygen consumption recorded until it returned to acclimation levels, in order to determine the oxygen debt of the fish. After approximately four measurements while the fish recovered, it was moved to the free swim trial arena. In order to determine background respiration, oxygen measurements were taken before and after each respirometry trial using a 600 second measurement period and otherwise the same settings. Background respiration remained stable during each measurement so an assumed linear growth between pre- and post-trial background respiration was used to determine the real oxygen consumption of each fish.

To determine U_{opt}, MO_2 (mg of Oxygen consumed per gram of fish mass per hour) was plotted against swim speed and the relationship was determined via a 2-factor exponential function (equation 1; Figure 2), a 3-factor exponential function (equation 2) or a 3-factor power function (equation 3), depending on which best fit the data. While the 3-factor power function as argued for in Roche et al. 2013 provided the best fit in 10/16 cases, we nonetheless found 3- or 2- factor exponential functions to be the superior fit for the remaining 6.

Equation 1:

$$MO_2 = a * e^{b*Swim\ speed}$$

Equation 2:

$$MO_2 = a + b * e^{Swim\ speed}$$

Equation 3:

$$MO_2 = a + b * swim\ speed^{c}$$

In these equations a, b and c represent constants.

With the data fitted to a curve, the cost of transport (COT) was determined for each by dividing the equations by swim speed.

Equation 4:

$$COT = \frac{a*e^{b*Swim\ speed}}{Swim\ speed}$$

Equation 5:

$$COT = \frac{a+b*e^{Swim\ speed}}{Swim\ speed}$$

Equation 6:

$$COT = \frac{a+b*swim\ speed^{c}}{Swim\ speed}$$

U_{opt} was defined as the speed at which COT is minimised (Figure 2) and was derived by setting the first derivative to zero.

3. Free swimming (U_{pref}) trial

After respirometry was completed, each fish was placed in a 103 cm diameter circular tank in order to determine U_{pref}. A 29 cm diameter circular opaque barrier was placed at the centre of the tank, with a hole drilled in the bottom through which a 15 cm standpipe (to maintain 15 cm water depth) was threaded. The barrier contained 21 holes, each with a diameter of 2.5 cm, in order to allow water to pass the barrier and reach the standpipe while excluding the fish. A circular counterclockwise water flow with a speed gradient from the outside to the centre of the tank was created using two water pumps, one Eheim pump with a flow rate of 1250 l h^{-1}, and one Eheim pump with a flow rate of 4164 l h^{-1}. Both pumps were connected to an outflow point on the outer edge of the swimming area consisting of a 1.65 cm diameter PVC pipe with nine 0.55 cm diameter holes drilled in a vertical line, in order to facilitate even flow through the water column. Inflow to the larger pump was connected to a similar PVC pipe with nine 1 cm diameter holes to allow water uptake, placed directly behind the outflow pipe on the outside edge of the swimming area. Inflow to the smaller pump was connected to the standpipe to prevent still water in the centre of the tank during trials (Figure 3). During acclimation periods, the standpipe was connected to a drain and seawater was allowed to flow into the tank continuously in order to maintain a constant ambient temperature. Fish were acclimated for 4-12 hours. Following acclimation, the smaller pump was reconnected and fish allowed one hour to acclimate to the new flow conditions. Fish were then recorded for one hour. Flow rate under trial conditions was recorded at 40 points of known coordinates (measured in cm) relative to the standpipe (designated as point 0,0), creating a heat map of water flow speed by averaging values between known speeds at equidistant measured coordinates (Equation 7).

Equation 7:

$$U_{xb,yb} = \frac{U_{xa,ya} + U_{xc,yc}}{2}$$

This was repeated until values of speed at every 5° around the tank were known. Data was then interpolated using the Akima package in R (Akima & Gebhardt 2022), producing a high-resolution set of coordinate data and allowing a circular plot of flow speed to be produced (Figure 4). Flow speed varied from a maximum of 67 cm s^{-1} directly in front of the pump outflow, to 0-2 cm s^{-1} in the centre of the swimming area. This represents a gradient of > 3 to < 0.5 bl s^{-1} for our fish, allowing them a wide range of water flow rates from which to choose their preferred swimming speed.

Data was collected for each pair of fish over three days. The “A” individual within a pair underwent respirometry on day 1 and a preferred swimming trial on day 2, then was placed alone into a holding tank to distinguish it from other study fish until day 3. The “B” individual within a pair underwent respirometry on day 2 and a preferred swimming trial on day 3. Immediately after completing the individual free swimming trial on day 3, the “A” fish was retrieved from the holding tank and placed back in the free swimming tank with the “B” fish. The two individuals were then allowed 4 hours to acclimate to the tank and to one another, at which point the small pump was reconnected. Following an additional 30 minutes of acclimation a one-hour paired preferred swimming trial was recorded.

Free swimming trials were recorded by a Sony X100 camera mounted approximately 2.5m above the tank at a frame rate of 30 fps. Videos were recorded as mp4 files and were subsequently converted to pv files for analysis using the animal tracking software Trex (Walter and Couzin, 2021). Trex was used to determine the position of fish in each video, with coordinate data exported in pixels. Data in pixels were then converted to cm coordinates as defined by the flow speed heatmap (Equation 8).

Equation 8:

$$x_{cm} = \frac{x_{pixels}}{cf} - \frac{sp}{cf}$$

Where x_{cm} is the x coordinate on the heatmap, x_{pixels} is the x coordinate as exported by Trex, cf is the conversion factor between cm and pixels as given by Trex (e.g. 1 pixel = 0.25cm) and sp is the x coordinate of the standpipe in pixels as given by Trex. For y coordinates, the equation was reversed as Trex sets 0,0 to the top right hand corner of the image (Equation 9).

Equation 9:

$$y_{cm} = \frac{sp}{cf} - \frac{y_{pixels}}{cf}$$

In paired trials, neighbour distance data was also exported from Trex and converted to centimetres by multiplying by the conversion factor. In order to find the speed of fish at each point in the trial according to their coordinates, heatmap coordinate data and trial coordinate data were each converted to separate spatial points data frames using the sp package in R (Bivand et al., 2013). Trial coordinate data was then interpolated to heatmap coordinate data using the dplyr package (Wickham et al., 2023), allowing speed data for the trial coordinate data to be extracted based on known speed values in the heatmap coordinate data. This data was converted to excel data using the clipr package (Lincoln, 2022).

Videos were also manually reviewed to assess the percentage of time fish spent steady swimming versus moving around the tank. Time spent steady swimming was defined as when the fish stayed in approximately the same position within the flow. Non-steady swimming was defined as when

a) The fish moved more than 90° (one quarter of the circumference of the tank) forward or backward in the tank in a continuous movement, while still facing into the flow
b) The fish turned around and swam with the flow, regardless of how far it swam with the flow
c) In paired trials, when fish overtook one another

Non-steady swimming times were then excluded before the modal swim speed for each trial was calculated.

4. Data analysis

4.1. U_{opt} and U_{pref}

All models were constructed in R (version 4.2.2). In order to determine whether U_{opt} had a significant effect on U_{pref}, a linear model was constructed using the lme4 and lmertest packages (Bates et al., 2015; Kuznetsova et al., 2017), with U_{pref} from individual trials as the resultant variable. The explanatory variables were U_{opt} and fish total length. Fish ID was not included as a random effect, as fish were only tested once. The interaction U_{opt}*fish total length was also included. Models with and without the interaction term were compared using Akaike's Information Criterion (AIC) to find the best fit model (Mazerolle 2023).

4.2. Individual and paired U_{pref}

In order to determine whether the presence of a conspecific would affect U_{pref} compared to when fish were alone, a linear mixed model was constructed using lme4 and lmertest (Bates et al., 2015; Kuznetsova et al., 2017). The resultant variable in this case was U_{pref}(paired), and the explanatory variables were U_{pref}(individual), U_{pref}(conspecific) (i.e. the U_{pref} of the fish each individual was paired with), neighbour distance, and fish total length. The interaction terms of U_{pref}(individual)*U_{pref}(conspecific), U_{pref}(individual)*neighbour distance, and U_{pref}(conspecific)*neighbour distance were also included. Fish ID, referring to whether the fish was tested for individual and paired Upref on subsequent days or on the same day, was included as a random effect in order to account for any effects of the time of testing. Pair ID was also included as a random effect. Models with and without all interaction terms and with and without the NND term were compared using AIC to find the best fit model (Mazerolle 2023). Graphs were plotted in the ggplot2 package (Wickham, 2016). A pairwise t test was used to compare means of Upref, Upair, and Uopt.

Results

1. Overview of results

A total of 16 fish were analysed for U_{opt} and individual U_{pref}. Of these, 14 were included in paired trials to assess paired U_{pref}. U_{opt} values ranged from 1.56 to 3.59 bl s^{-1}, with a mean value of 2.30±0.44 bl s^{-1}. Individual U_{pref} ranged from 0.16 to 1.56 bl s^{-1}, with a mean value of 0.78±0.42 bl s^{-1} (Figure 5). In paired trials, U_{pref} ranged from 0.18 to 2.63 bl s^{-1}, with a mean value of 0.73±0.62 bl s^{-1}. U_{crit} ranged from 3.05 to 4.08 bl s^{-1}, with a mean value of 3.72±0.34 bl s^{-1}. U_{opt} occurred at a mean value of 62% of U_{crit}, while U_{pref} occurred at 21% of U_{crit} on average.

2. U_{opt} versus U_{pref}

The pairwise t test revealed a significant difference between U_{opt} and U_{pref} ($p < 0.001$), with U_{opt} being significantly greater (t statistic = 6.58). The final best linear model did not retain the interaction between U_{opt} and total body length (Table 1). In addition, neither U_{opt} nor total body length were significantly correlated with U_{pref}, indicating that U_{pref} in *R. vacca* is not strongly influenced by U_{opt}.

3. Individual versus Paired U_{pref}

Pairwise t testing found no significant difference between individual and paired U_{pref} ($p = 0.176$, t statistic = -1.43), though paired U_{pref} was also significantly lower than U_{opt} ($p < 0.001$, t statistic = -7.15). Neither interaction with nearest neighbour distance was retained in the final model, though the interaction between individual and partner U_{pref} was retained (LRT $p < 0.001$) (Table 2). Both individual ($t = 3.034$, $p = 0.009$, $r^2 = 0.30$) and partner ($t = 3.155$, $p = 0.007$, $r^2 = 0.31$) U_{pref} were positively correlated with paired U_{pref}. Mean nearest neighbour distance was not significantly correlated with paired U_{pref}. In addition, the interaction term between individual and partner U_{pref} was negatively correlated with paired U_{pref} ($t = -2.43$, $p = 0.021$, $r^2 = 0.53$), indicating a reduced effect of individual Upref at high partner U_{pref} (Figure 6).

Discussion

Determining a movement strategy is a key aspect of behaviour for all mobile animals. While energy needs are a vital consideration when selecting a movement strategy, other aspects of an animal's ecology such as their abiotic and social environment, behavioural "personality," and feeding strategy may also impact how an animal chooses to move within its environment. Our study provides evidence that in marine generalist species such as the pile perch *Rhacochilus vacca*, optimising energy usage per distance travelled may not be the most important factor when considering movement strategy. U_{opt} in this species was significantly higher than both individual and paired U_{pref}, and also did not explain significant variance in individual U_{pref}. We also present evidence that an individual's social environment may affect swim speed in *R. vacca*. Both individual U_{pref} and partner U_{pref}, as well as the interaction between the two, were significantly correlated with U_{pref} when swimming in pairs, indicating that fish may adjust individual U_{pref} in order to school with a conspecific. Our study provides evidence that marine generalist species may prioritise other ecological considerations over optimising energy consumption when determining U_{pref}.

Previously published work on the relationship between U_{opt} and U_{pref} has focused on the migratory species *Salvelinus fontinalis* (Tudorache et al., 2011). In this species, U_{pref} appears to track U_{opt} closely. This represents an advantageous strategy when selecting a sustained swim speed for covering long distances, and so is an intuitive finding for migratory species. However, in a marine coastal generalist such as *R.vacca*, other factors are likely to confound the relationship between U_{opt} and U_{pref}. The appropriately-named pile perch frequents complex habitats around coastlines and artificial structures such as piers (Alevizon, 1975; Allen and Pondella 2006). Behavioural tasks associated with spatially complex and densely populated habitats, like foraging and avoiding predators, require rapid changes in swim speed and direction. These behaviours are then likely to be prioritised over swimming at a speed which minimises cost of transport, particularly if that speed is impractically high for an individual's environment (Killen et al., 2007). It may therefore be of greater advantage for species such as *R. vacca* to accept inefficient energy costs of movement so as to improve their chances of finding food or a mate, manoeuvre around obstacles, and avoid predators by reducing their U_{pref} below their U_{opt}.

Metabolic rates may also influence U_{pref} in species that do not need to optimise energy use over long distances. The lumpsucker *Cyclopterus lumpus*, a benthic species occupying similar habitats to *R. vacca*, avoids Swimming at U_{opt} while foraging and prefers to remain motionless if given the opportunity and provided a minimum density of prey is available (Killen et al., 2007). This study speculates that maintaining low swimming speeds may allow fish to maximise their aerobic scope at a given time, particularly in fish whose aerobic scope is limited such as *C. lumpus*. While we did not measure maximum metabolic rate in *R. vacca* and therefore cannot determine aerobic scope, our calculations indicate that U_{opt} represents a much greater proportion of U_{crit} than U_{pref} does in this species. The scope for an increase in activity when moving at U_{opt} is therefore significantly reduced compared to when moving at U_{pref}, which may represent a survival cost when attempting to escape predators, for example see (Wood, 1991).

Another factor that appears to influence the movement decisions of *R. vacca* is an individual's social environment. Preferred swim speed when swimming with a conspecific partner was significantly affected by both individuals' U_{pref}. Further, the relationship between individual and paired U_{pref} changed from a positive to a negative correlation when the partner's individual U_{pref} was very high. This indicates that fish may be more likely to sacrifice their own optimal swimming to school with a partner when that partner has a more extreme phenotype in terms of U_{pref}. This has obvious advantages in terms of remaining in groups, which may help individuals to avoid predators, find food, and find mates (Pitcher et al., 1982; Wright et al., 2006). Physiological costs of increasing U_{pref} may therefore be worthwhile in allowing this social species to remain with a conspecific. Studies of performance in larger groups as well as in arenas of different shapes would be advantageous in confirming this, however, as vortices between conspecifics and effects of arena shape also play a role in flow dynamics and therefore energy use (Marras et al., 2015; Zheng et al., 2022). Our study was also limited in the number of fish that we were able to observe, with only seven pairs. Larger studies would be helpful in generalising our results to the population level for *R. vacca* and to other marine generalist species.

Conclusions

While optimising energy usage may be a critical concern for some migratory species, other ecological and physiological factors may influence volitional movement strategy in species living in more complex environments. Our study shows, possibly for the first time, that a marine generalist species prioritises slower movement over optimal energy use. This likely confers an advantage when living in a complex habitat, and allows this species to find food and avoid predators. In addition, we found that in at least this social fish species, movement strategy may be altered by the presence of a conspecific, indicating that moving in groups confers significant advantages that may confound individual physiological or behavioural optima. Our study adds novel insights to the study of relationships between energy use and behaviour, and emphasises the importance of ecological context in determining animal behaviour. Such studies may also provide a basis for determining optimal conditions for animals in captivity, as well as the behavioural impacts of changing ecological conditions.

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Figures and tables

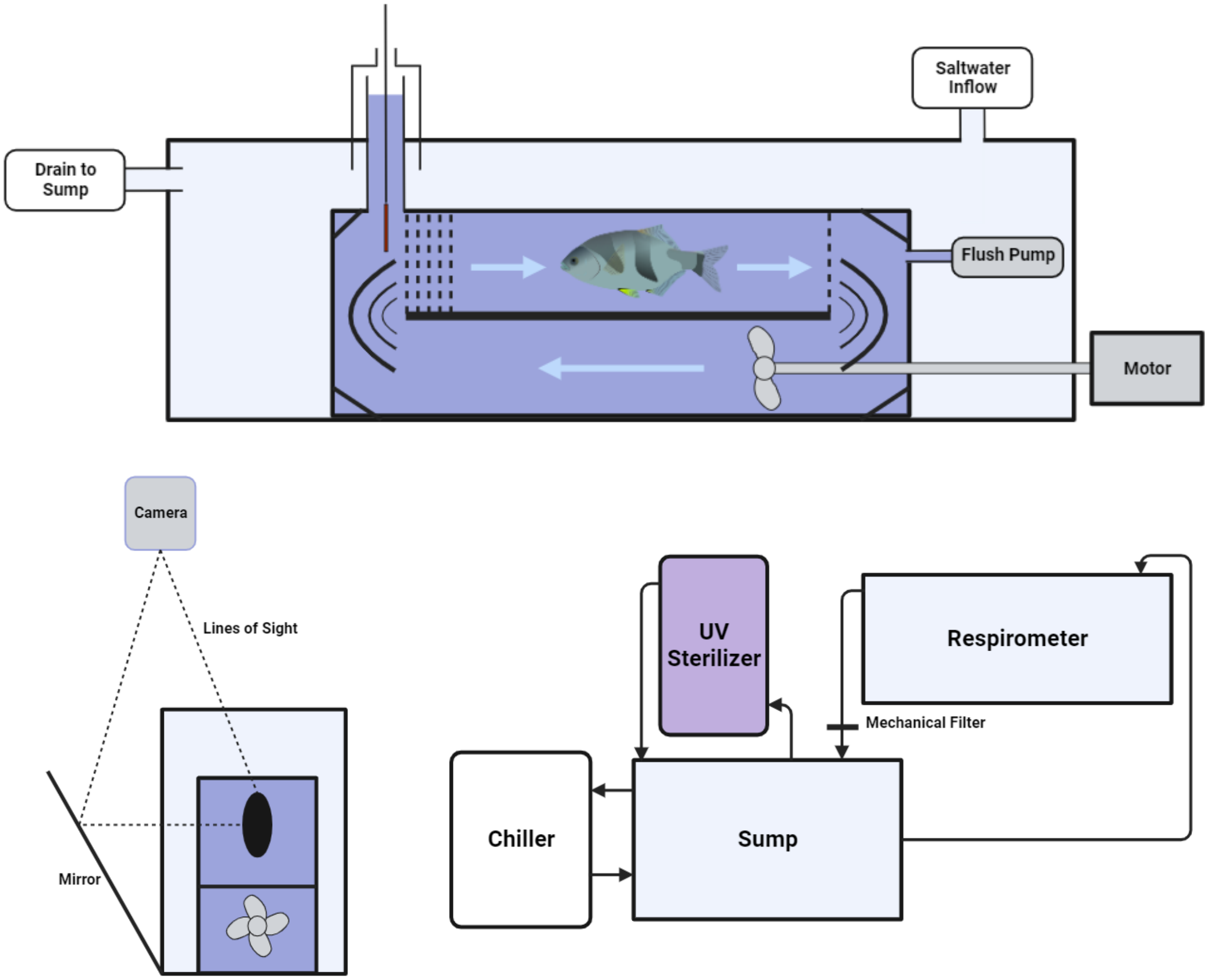

Figure 1. Diagram showing setup of respirometry tank from side (top) and front (bottom left) perspectives, and overall setup including temperature and bacterial control mechanisms (bottom right).

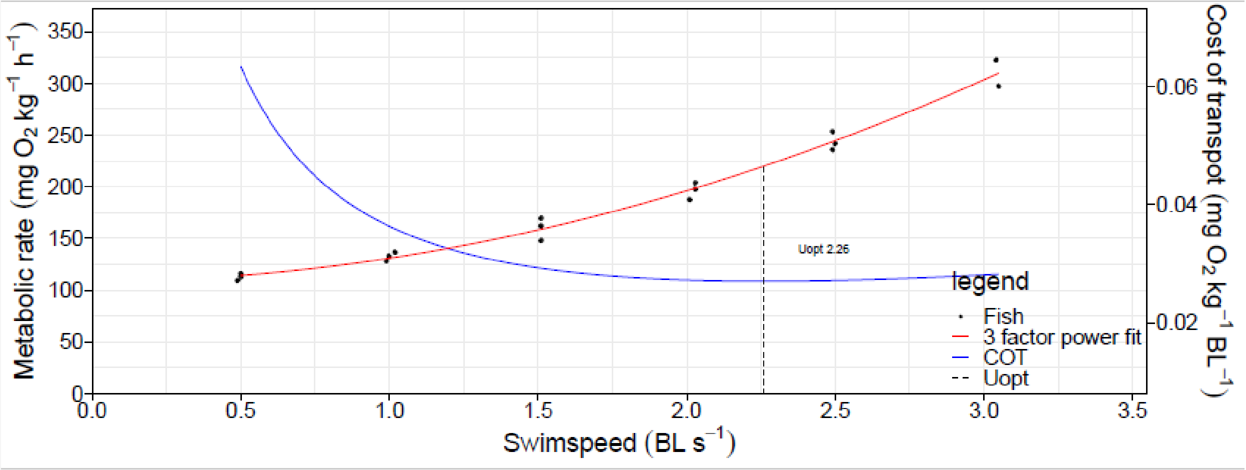

Figure 2: Example of U_{opt} calculation. The dots represent the MO_2 measurements for a fish at a certain speed and the red line is the 3 factor exponential fit (both use the left Y axis). The blue line represents COT using the right Y axis. The dashed line is U_{opt}.

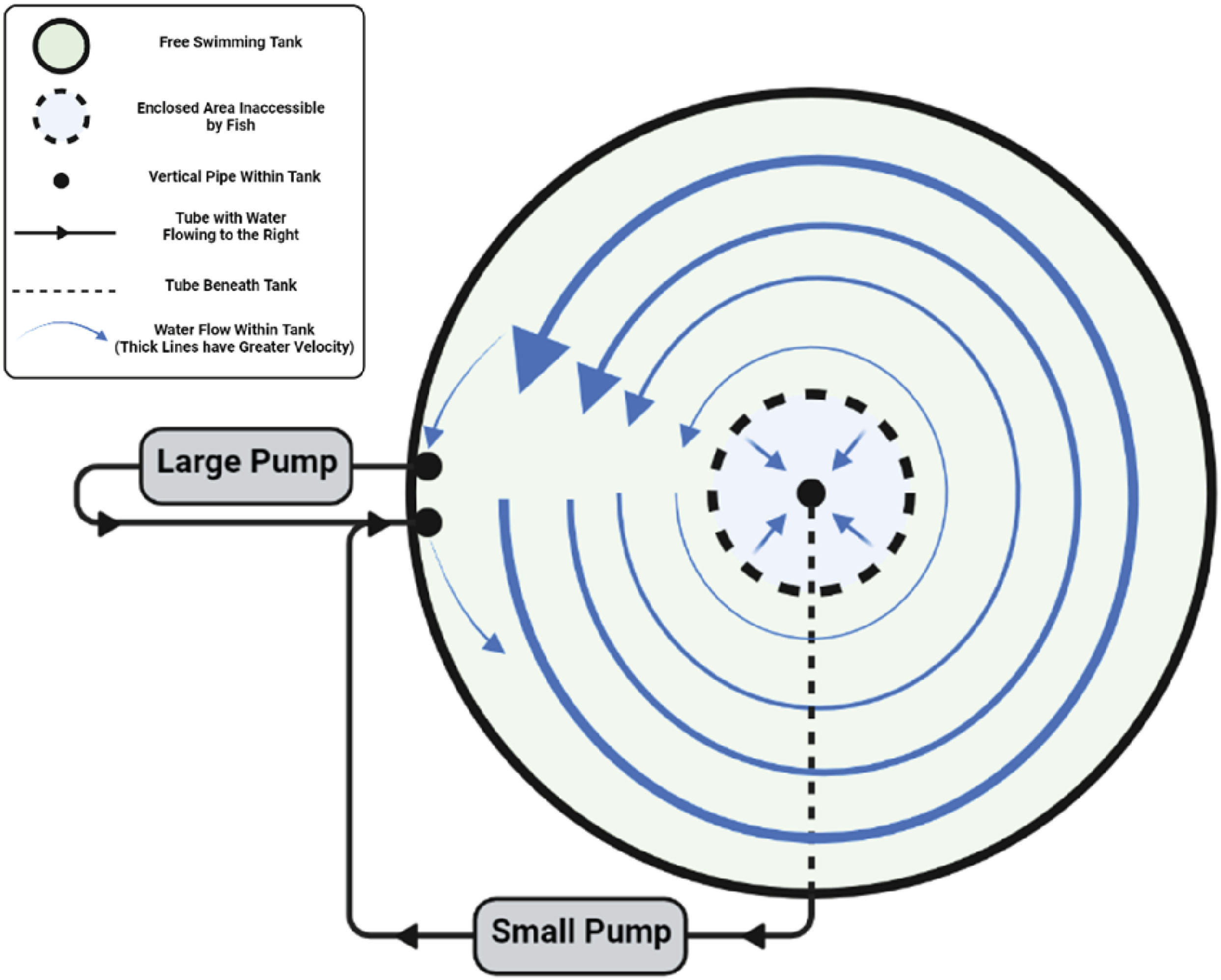

Figure 3. Diagram showing setup of free-swimming tank during Upref swimming trials.

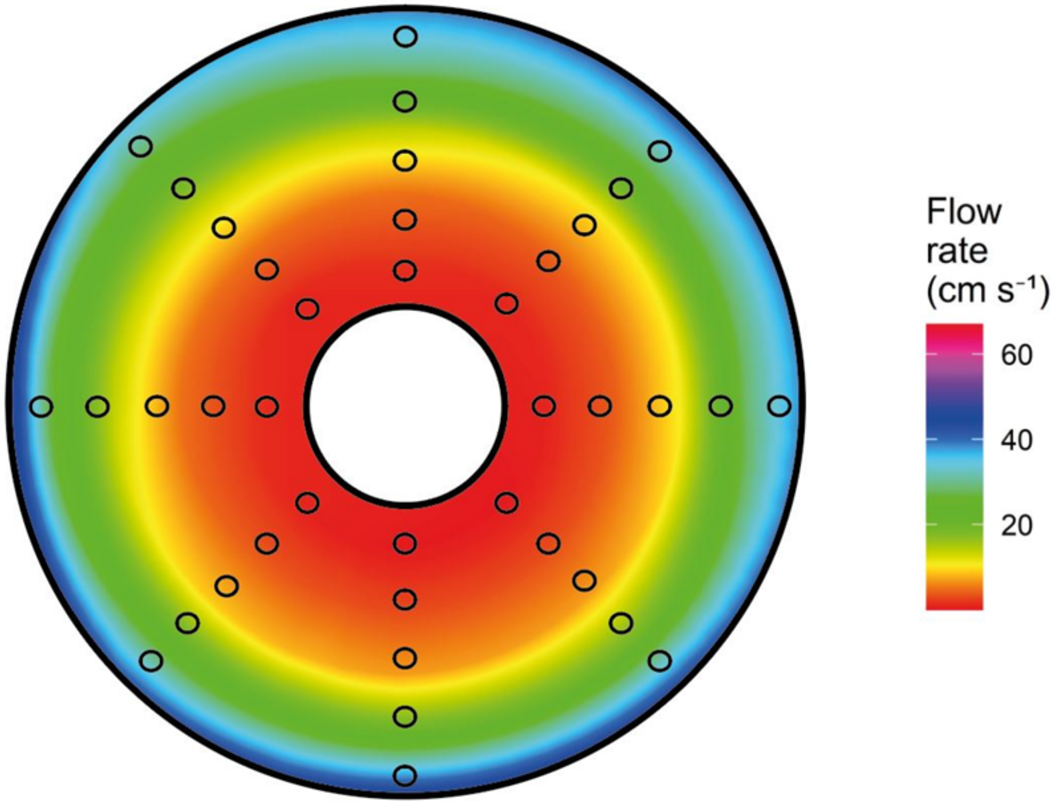

Figure 4. Heatmap showing flow rate in free-swimming tank

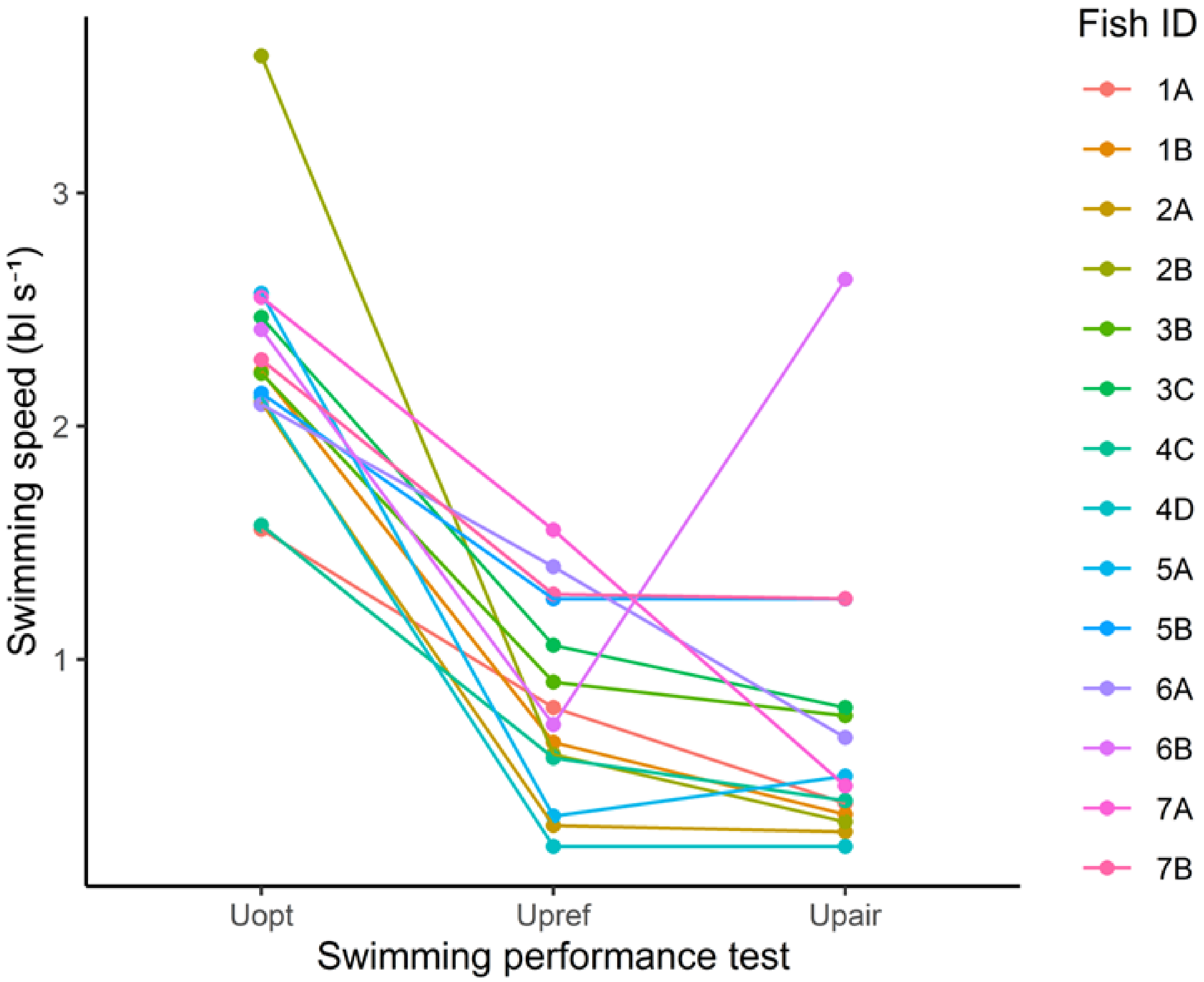

Figure 5. Optimum swimming speed (Uopt), individual preferred swimming speed (Upref), and preferred swimming speed when in a pair (Upair) of individual *Rhacochilus vacca*.

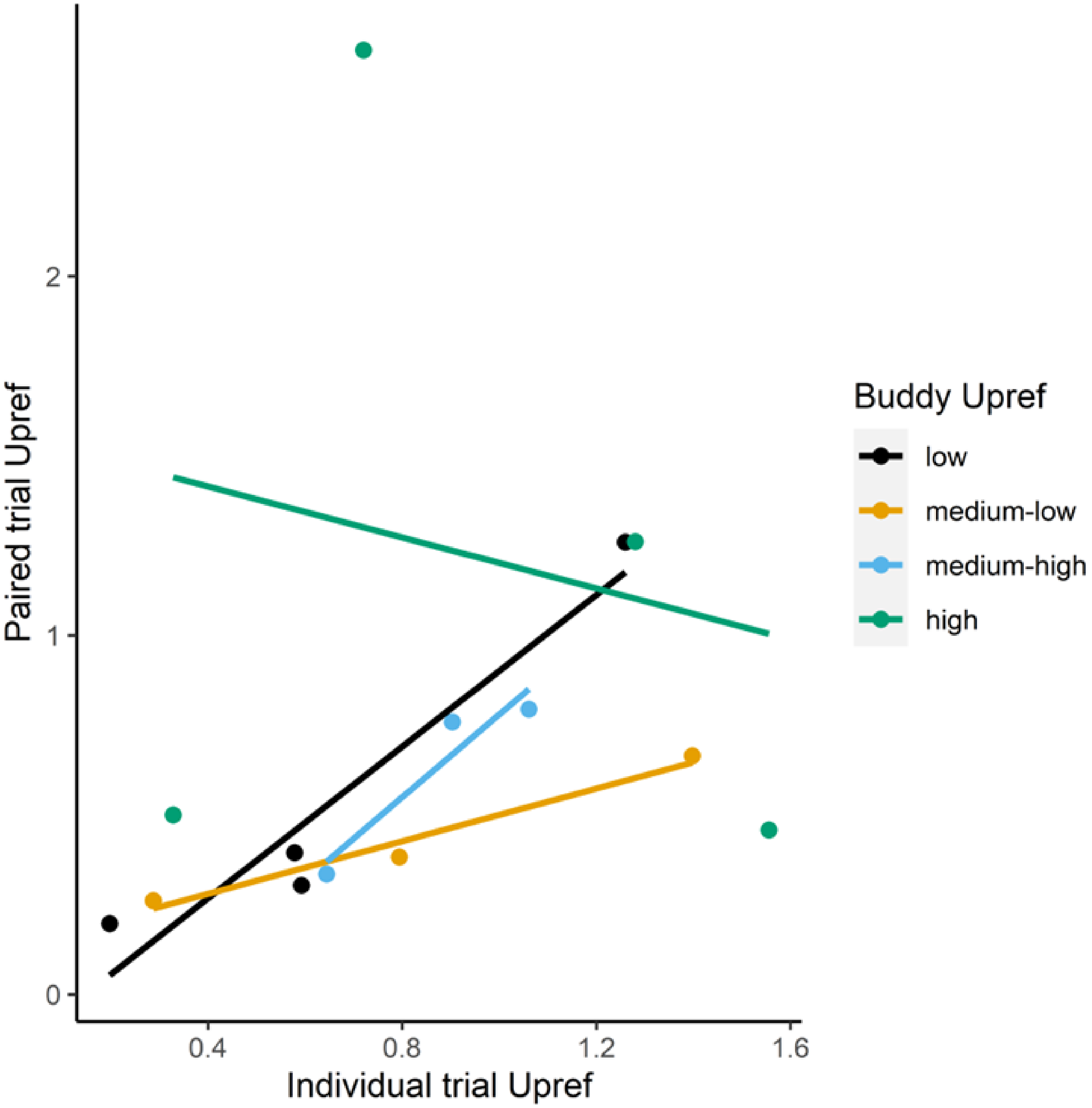

Figure 6. Positive relationship between paired and individual preferred swimming speed (Upref) at low conspecific Upref, but negative relationship at high conspecific Upref.

Table 1. Results of linear model investigating variables affecting individual Upref

	Estimate	Std. Error	t value	Pr(>|t|)	r^2_m	r^2_c
					0.08	0.08
(Intercept)	0.039	0.843	0.046	0.964		
Uopt	0.057	0.133	0.43	0.674		
Length	0.048	0.043	1.129	0.279		

Table 2. Results of linear mixed model investigating variables affecting paired Upref

	Estimate	Std. Error	df	t value	Pr(>|t|)	r^2_m	r^2_c
						0.53	0.67
Intercept	-1.288	0.2743	9.4433	-4.695	<0.001***		
Individual Upref	0.957	0.3156	8.9527	3.034	0.014*		
Buddy Upref	0.993	0.3148	8.7832	3.155	0.012*		
Individual Upref * Buddy Upref	-0.786	0.3237	8.5424	-2.43	0.039*		