

Appendix B from R. Holzman et al., “Functional Complexity Can Mitigate Performance Trade-Offs”

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Suction Index Predicts Peak Flow Speed at the Mouth

The suction index is based on a biomechanical model that predicts the maximal buccal pressure drop a fish is capable of producing as a function of the transmission of force from the epaxial muscles (proportional to the cross-sectional area of that muscle [CSAE]) to elevate the cranium and expand the buccal cavity (Carroll et al. 2004; Holzman et al. 2008c). Following Carroll et al. (2004), the suction index (SI) incorporates measurements of area of the buccal cavity (B_{area} , equal to the product of morphological gape width and buccal length), the CSAE, and the lengths of the epaxial muscles' in- and out-levers (L_{in} and L_{out} , respectively), following the equation

$$\text{SI} = \frac{\text{CSAE} \times (L_{\text{in}}/L_{\text{out}})}{B_{\text{area}}}. \quad (\text{B1})$$

Species values of suction index were measured as described by Collar and Wainwright (2006). Components of buccal cavity area are only weakly correlated during evolution in most centrarchid lineages (Collar and Wainwright 2006; Revell and Collar 2009).

We used the suction index to predict the peak flow speed each individual can produce at its mouth. Hydrodynamic considerations (the Bernoulli principle; Vogel 1994; Van Wassenbergh et al. 2006a), as well as empirical measurements (Higham et al. 2006b; Holzman et al. 2008c) indicate that squared peak flow speed is correlated with peak buccal pressure (and thus with suction index). We used a two-point interpolation using empirical data on peak flow speed in bluegill sunfish and largemouth bass (Higham et al. 2006a), two morphological and ecological extremes within Centrarchidae that also possess the highest and lowest suction indexes in the group (Collar and Wainwright 2006). Following this interpolation, we estimated the relationship between suction index and peak flow speed (U_{max}) as

$$U_{\text{max}} = 1.63 + 1.5044\sqrt{\text{SI} - 0.05}. \quad (\text{B2})$$

The relationships between pressure and flow speed are conserved both within and between bluegill and bass (Higham et al. 2006a), as well as within an ontogenetic series within bluegill (Holzman et al. 2008c), supporting our assumption that that pattern is conserved across the other species. However, this interpolation likely underestimate of the true diversity in flow speeds across Centrarchidae. We view this simplification as a conservative factor in our analysis of evolutionary dynamics, because it underestimates the variation in the complex system, contrary to the $H_{(1)}$ hypothesis.

Kinematics of Prey Capture

Suction feeding strikes of individual fish from 15 centrarchid species were filmed at 500 frames per second using a high-speed digital video camera (NAC Memrecam Ci, Tokyo). For each species, 1–3 individuals were filmed in lateral view, and for each individual we sampled 6–10 strikes on ghost shrimp under standardized experimental conditions (see table B1). Filming trials complied with all guidelines for the use and care of animals in research at the University of California, Davis.

Video sequences were analyzed using DLTdataviewer2 (Hedrick 2008), a toolbox for automated kinematic analysis that runs in MATLAB (MathWorks, Natick, MA). A frame-by-frame analysis was conducted for each sequence, starting 10 frames before the onset of gape expansion and ending 10 frames after the fish started closing its mouth. We recorded the spatial position of landmarks on the fish and prey that allowed us to calculate

gape size, the location of the mouth's center, and the distance between the prey and the predator. We also tracked the depression of the hyoid and the angle of the head (relative to the body axis) throughout each strike. During the mouth-opening phase of each strike, we determined ram speed (speed of the body in the earthbound frame of reference), jaw protrusion speed (speed of the mouth center with respect to the body), and mouth displacement speed (the speed of the center of the mouth in the earthbound frame of reference). We also recorded maximal gape, the distance between the predator and the prey at the onset of mouth opening, and the time between the onset of mouth opening and peak gape (referred to as time to peak gape), the time of peak hyoid depression, and the time of peak head elevation. Following feeding trials, each fish was measured for standard length (measured from the tip of the snout to the posterior end of the last vertebra). Species values for all kinematic variables were taken as the means all sampled individuals weighted by the number of feeding trials.

A Hydrodynamic Model of Aquatic Suction Feeding Performance

We were interested in the role of complexity in determining performance trade-offs in suction feeding, an objective that warranted a method to quantify the contribution of each underlying trait to the capacity of fish to capture prey using suction. We used observed values of previously identified performance-determining traits to parameterize a model of water flow in front of a suction feeding fish's mouth and around the prey (Holzman et al. 2007; Wainwright and Day 2007; Holzman and Wainwright 2009). This enabled us to predict feeding success on attached and evasive prey and the contribution of each underlying trait to overall performance. In essence, we view our hydrodynamic model as a way to determine the performance gradients for functional components involved in suction feeding based on an empirically and computationally validated set of physical equations (Holzman et al. 2007; Wainwright and Day 2007; Van Wassenbergh and Aerts 2009). The hydrodynamic model provides a quantitative framework for generating and testing mechanistic hypotheses and to determine the inherent trade-offs within this system. Subsequently, predictions that follow from model output have been tested experimentally (Holzman et al. 2007) or using field data (this study).

The hydrodynamics that govern the forces exerted on the prey during a suction feeding strike are laid out in detail in Wainwright and Day (2007). These forces can be used to predict the relative motion of the prey and the mouth during a suction feeding strike, based on a set of boundary conditions that characterize the prey and describe the kinematics of the mouth and flow speed during the strike. As such, simulations that vary the boundary conditions can be used to investigate the effects of morphological, behavioral, and kinematic diversity on prey capture performance for different prey types.

Under this framework, prey capture can be defined as the case where the distance between the mouth and the prey turns negative while the mouth is opened. That distance is a time-dependent function of the speed of mouth displacement toward the prey, the speed of prey movement and its direction (toward or away from the mouth), and the strike initiation distance (the predator-prey distance at the time of strike initiation). Mouth displacement speed is a function of ram, jaw protrusion, and cranial elevation, and it is easily observed (e.g., from high-speed videos of feeding strikes). The speed of the prey (and the direction of its motion) is determined based on the forces exerted on the prey, which are used to calculate its trajectory. In general, the total force exerted on the prey is the sum of drag force, acceleration reaction force, pressure gradient force, swim forces, and gravitational forces (the latter will be ignored through the current discussion). These forces are affected from the interaction of multiple mechanisms, which are integrated using the hydrodynamic model. Once these forces are calculated and summed in small increments of time, it is possible to solve for the acceleration, speed, and movement of the prey and determine the strike's outcome—prey capture or escape.

The hydrodynamic force exerted on the prey results from the differential in speeds and accelerations between the prey and the water around it, as well as from a gradient of flow across the prey. From the predator's perspective, changes to water speed around the prey can be driven by the temporal patterns of flow at the mouth orifice (flow increasing during the strike), by the displacements of the mouth toward the prey (moving the mouth center, where flow is strong, toward the prey), and through mouth opening (that increases the reach of suction flows). The gradient of flow velocity across the prey depends on the size of the mouth and the distance between the prey and the mouth center, which jointly determine the rate of decay of flow speed with increasing distance from the mouth. These effects are mediated by prey size and length, as well as drag and added mass coefficients, which summarize the small-scale interactions between the unsteady flow field and the solid object within it. However the effects of those mechanisms are often nonlinear and depend on the state of other variables. The

force model is a useful tool for integrating those effects and quantifying the contribution of each mechanism to strike success.

Model Inputs

As detailed above, the determinants of the forces exerted on the prey are the speeds and accelerations of water around the prey. Under passive flow regime (flow into a wide orifice, a characteristic state in aquatic suction feeding) those patterns can be inferred from the flow at the mouth center, given information on the size of the mouth and the distance between mouth center and the prey. Our hydrodynamic model was parameterized with morphological and kinematic data collected from 15 species of the North American freshwater fish radiation Centrarchidae. The kinematic data were gathered from high-speed video recording of fish capturing prey, and the morphological data were measured from cleared and stained specimens. Using data from each species as input for the hydrodynamic model, we simulated the expected success of each species when suction feeding. In these simulations, the outcome of each strike (prey capture or escape) was determined by the net hydrodynamic forces acting on the prey (equal to the total force exerted by predatory suction flows less the prey's escape force or its attachment force to the substrate). The integral for those forces over time ultimately determines whether an attached prey will be dislodged from its holdfast or whether an escaping prey will be drawn into the mouth (Van Leeuwen and Muller 1984; Weihs and Webb 1984; Holzman et al. 2007, 2008a; Holzman and Wainwright 2009). Thus, we describe aquatic predator-prey interactions using a time-dependent simulation that depicts the hydrodynamic interaction between a suspended prey item in the water column and the flow around it, and we use this framework to isolate the effect of each kinematic and morphological variable on the interaction's outcome.

Each run of the model simulated a single predator-prey encounter in which the observed timings of cranial kinematics (e.g., the opening of the mouth and movement toward the prey) served as input to estimate the spatiotemporal pattern of flow in front of the mouth of suction feeding fish (Day et al. 2005; Higham et al. 2006a; Holzman et al. 2008c) and the resulting suction-induced forces exerted on the prey. The model calculates the movement of the prey in small time increments based on the forces exerted on the prey by the suction flows (drawing the prey into the mouth) and on the swimming forces produced by the prey (moving it away from the mouth). The model outcome was scored as prey capture if the distance between the prey and the predator became negative (i.e., the prey crossed the gape line) before the jaws began to close. Based on the same criteria, the outcome of a strike was an escape if the distance between predator and prey remained positive until the jaws closed.

Traits That Affect Suction Performance

The force a fish exerts on its prey is a function of its ability to produce flow speeds and accelerations in the earthbound frame of reference (Wainwright and Day 2007). For each individual fish in this study, we estimated the peak flow speed it can produce as a function of its suction index, which is a measure of a fish's maximal capacity to produce suction pressure based on its cranial morphology. Given a fish's maximum capacity to generate water flow, the success of any given strike is also affected by the extent of mouth opening (Wainwright et al. 2007), strike efficiency (i.e., the ability to time the strike to produce the maximal force on the prey; Holzman et al. 2007), and mouth displacement speed (the sum of jaw protrusion and swimming speed; Holzman et al. 2008a). Therefore, we also measured jaw protrusion speed, ram speed, and maximal gape from high-speed videos of feeding strikes. Using these data as input for the hydrodynamic model (Holzman et al. 2007), we then estimated for individual fish the maximum suction-induced force and the spatial reach of the flow (defined as the distance from the center of the mouth where the flow is <5% of the flow at the mouth aperture), as well as the simulated success in capturing attached and evasive prey. The use of the hydrodynamic model enabled us to quantitatively assess the independent effects of flow speed, jaw protrusion speed, and gape on these measures of feeding performance.

Table B1. Species' means for gape size, suction index, standard length (SL), and the number of fish used for the analysis of prey capture kinematics across centrarchid species

Species	Gape size (mm)	Suction index	SL (mm)	No. fish filmed
<i>Acantharchus pomotis</i>	24.8	.10	124	1
<i>Centrarchus macropterus</i>	18.7	.07	133	3
<i>Enneacanthus chaetodon</i>	3.8	.21	46	3
<i>Enneacanthus obesus</i>	10.8	.22	67	3
<i>Lepomis cyanellus</i>	17.8	.14	132	3
<i>Lepomis gibbosus</i>	9.7	.33	110	2
<i>Lepomis gulosus</i>	15.7	.08	171	2
<i>Lepomis macrochirus</i>	16.7	.4	157	3
<i>Lepomis megalotis</i>	9.4	.39	111	3
<i>Lepomis microlophus</i>	13.1	.24	154	3
<i>Lepomis miniatus</i>	13.4	.29	106	2
<i>Lepomis symmetricus</i>	11.7	.26	79	3
<i>Micropterus dolomieu</i>	18.2	.08	157	3
<i>Micropterus salmoides</i>	30.0	.05	206	3
<i>Pomoxis nigromaculatus</i>	32.4	.12	225	1

Literature Cited Only in Appendix B

- Hedrick, T. L. 2008. Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspiration and Biomimetics* 3:034001.
- Revell, L. J., and D. C. Collar. 2009. Phylogenetic analysis of the evolutionary correlation using likelihood. *Evolution* 63:1090–1100.
- Van Leeuwen, J. L., and M. Muller. 1984. Optimum sucking techniques for predatory fish. *Transactions of the Zoological Society of London* 37:137–169.
- Van Wassenbergh, S., P. Aerts, and A. Herrel. 2006a. Hydrodynamic modelling of aquatic suction performance and intra-oral pressures: limitations for comparative studies. *Journal of the Royal Society, Interface* 3:507–514.