

RESEARCH ARTICLE

An integrative modeling approach to elucidate suction-feeding performance

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SUMMARY

Research on suction-feeding performance has mostly focused on measuring individual underlying components such as suction pressure, flow velocity, ram or the effects of suction-induced forces on prey movement during feeding. Although this body of work has advanced our understanding of aquatic feeding, no consensus has yet emerged on how to combine all of these variables to predict prey-capture performance. Here, we treated the aquatic predator–prey encounter as a hydrodynamic interaction between a solid particle (representing the prey) and the unsteady suction flows around it, to integrate the effects of morphology, physiology, skull kinematics, ram and fluid mechanics on suction-feeding performance. We developed the suction-induced force-field (SIFF) model to study suction-feeding performance in 18 species of centrarchid fishes, and asked what morphological and functional traits underlie the evolution of feeding performance on three types of prey. Performance gradients obtained using SIFF revealed that different trait combinations contribute to the ability to feed on attached, evasive and (strain-sensitive) zooplanktonic prey because these prey types impose different challenges on the predator. The low overlap in the importance of different traits in determining performance also indicated that the evolution of suction-feeding ability along different ecological axes is largely unconstrained. SIFF also yielded estimates of feeding ability that performed better than kinematic traits in explaining natural patterns of prey use. When compared with principal components describing variation in the kinematics of suction-feeding events, SIFF output explained significantly more variation in centrarchid diets, suggesting that the inclusion of more mechanistic hydrodynamic models holds promise for gaining insight into the evolution of aquatic feeding performance.

Key words: functional morphology, performance, Centrarchidae, diet, suction force, predator–prey interaction.

INTRODUCTION

Suction feeding is by far the most commonly used mechanism of prey capture in ray-finned fishes, and yet this large group of vertebrates shows vast diet diversity (Bellwood et al., 2006; Lauder, 1982; Lauder, 1985; Wainwright and Bellwood, 2002; Westneat et al., 2005). This trophic diversity is presumably supported by functional diversity, where species exhibit skull morphologies and feeding behaviors that lead to variation in prey-capture performance. Considerable effort has been directed at understanding the functional links between evolutionary changes in the suction-feeding mechanism, feeding performance and diet. For example, many insights have been made on the relative use of ram speed and suction during prey capture (Higham, 2007; Nemeth, 1997; Norton and Brainerd, 1993; Tran et al., 2010; Wainwright et al., 2001), and trade-offs have been identified between aspects of the suction-induced flow that lead to differential prey-capture performance (Carroll and Wainwright, 2009; Van Leeuwen and Muller, 1984; Van Wassenbergh et al., 2007; Werner, 1977).

One key to understanding suction-feeding performance is the interaction between the suction flow field generated by a predator and the body of the prey (Wainwright and Day, 2007). Rapid mouth opening and buccal cavity expansion generate water flow and hydrodynamic forces that overwhelm the defenses of the prey, drawing it into the predator's mouth. A combination of modeling

and empirical measurements have revealed that the hydrodynamic force exerted on prey is dominated by the force resulting from the induced pressure gradient in front of the fish's mouth (Holzman et al., 2008c; Holzman et al., 2007; Wainwright et al., 2007; Wainwright and Day, 2007). Although species differ in the capacity to generate suction flow velocity (Carroll and Wainwright, 2009; Carroll et al., 2004; Collar and Wainwright, 2006; Higham et al., 2006a; Van Wassenbergh et al., 2006), several additional factors contribute to the ability of the predator to exert hydrodynamic forces on the prey (Fig. 1). One such factor is the ability to time the approach towards the prey so that the prey experiences the period of fastest-changing flow velocity, which generally requires that the predator intercepts the prey within a window of only approximately 2 ms (Holzman et al., 2007). In addition, fast mouth displacement towards the prey (*via* jaw protrusion, body ram or their combination) will increase the acceleration of flow around the prey by rapidly moving the source of the flow closer to the prey (Holzman et al., 2008c). Also, the size of the mouth aperture affects the spatial gradient of flow because the spatial reach of the flow is proportional to the size of the mouth (Day et al., 2005); smaller mouths produce a steeper velocity gradient that increases the forces experienced by the prey (Skorczewski et al., 2010; Wainwright and Day, 2007). The complexity of predicting prey-capture performance (Fig. 1) is heightened by the diversity of strategies that prey use to avoid

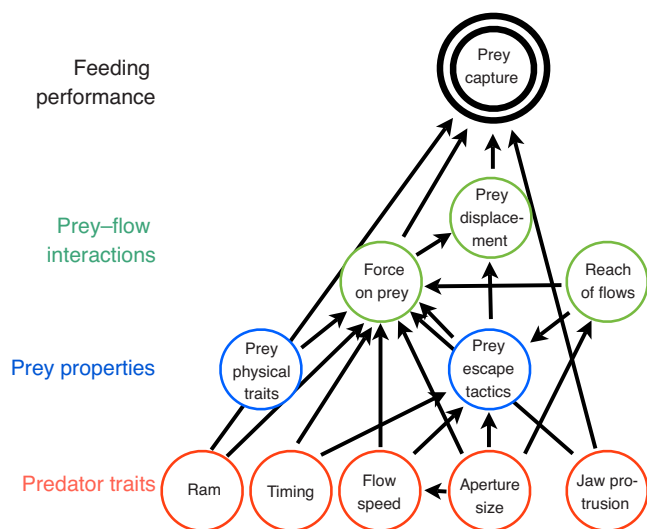


Fig. 1. Suction-feeding performance is determined by the complex interaction between the body of the prey and the suction-induced force field (SIFF) generated by a predator. Key determinants in this interaction include prey properties, predator traits and their interactions, and the spatial and temporal gradients in flow velocity, strike accuracy, jaw protrusion, body ram and the size of the mouth aperture. Note the complex pathways leading to prey capture, including indirect effects, determinants that affect more than one aspect of performance and performances that are determined by multiple determinants. Those interactions are further complicated by the diversity of strategies that prey use to avoid capture, such as clinging to a holdfast or swimming fast enough to overcome the suction flow.

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In this paper we integrate several factors that determine suction-feeding performance into a model of the suction-induced force field (SIFF), which we have implemented in user-friendly MATLAB code. SIFF builds on previously published evaluations of the hydrodynamic interaction between suction flows and prey (Wainwright and Day, 2007). Here we use SIFF to estimate suction-feeding performance, defined as the success rate of capturing prey given the hydrodynamic properties of the predator-induced flow field and the prey. SIFF uses information on gape kinematics (diameter and position as a function of time) and the temporal flow pattern at the mouth to calculate the spatial and temporal patterns of flow at the location of the prey, based on the distance between the prey and the predator's mouth at the time of peak gape. By specifying prey parameters for a given feeding event such as prey shape, size, density and behavior (e.g. swimming, being attached or free-floating), SIFF accounts for the interaction between the water and the prey and permits the calculation of forces exerted on the prey, speed and acceleration of prey movement, and the distance between prey and predator through the strike. Thus, SIFF integrates the effects of morphology and kinematics that determine the temporal patterns of mouth opening, mouth displacement (through ram, jaw protrusion or head elevation) as well as the resulting flow speed with the behavior of the prey. SIFF output is a time-dependent vector of predator-prey distances that are based on the net forces exerted on the prey (the sum of suction forces and the opposing prey-generated forces). We used these distances as proxies for prey capture, which we define as the case where the distance between the prey and predator turns negative (i.e. the prey entered the predator's mouth) while the mouth is still open. Running the model with different

parameters for a prey's response enables us to estimate feeding performance for each species.

Our objectives in this paper were to: (1) explore the morphological, kinematic and functional basis of suction-feeding performance evolution in centrarchid fishes feeding on three types of prey – evasive, attached and zooplankton; and (2) make SIFF available to studies of suction-feeding performance. Specifically, we used SIFF to estimate several aspects of feeding performance in 18 species of centrarchid fishes based on measured values for several key morphological and kinematic variables. We then applied phylogenetic comparative methods to estimate the correlations between SIFF-inferred performance and observed patterns of prey use in natural populations. We compared these correlations with those based on statistical description of strike kinematics, derived from a principal components analysis on commonly measured kinematic variables. We further asked which trait combinations contribute to the ability to feed on the three types of prey and evaluate the extent to which these prey impose correlated demands on the feeding fish. The paper is accompanied by MATLAB code that implements SIFF for attached, evasive and zooplankton prey (available at http://www.iui-eilat.ac.il/faculty/roi_SIFF/roi_SIFF.aspx and http://www.eve.ucdavis.edu/~wainwrightlab/SIFF_web_page/SIFFnew.html).

MATERIALS AND METHODS

An overview of the framework

SIFF uses a set of parameters that characterize the prey and describe the kinematics of the mouth and flow speed during the strike (Table 1) to predict the motion of the prey relative to the mouth during suction feeding (Holzman et al., 2007; Wainwright and Day, 2007). In this study, we varied SIFF input parameter values based on measured morphology and strike kinematics of centrarchid species to investigate the effects of morphological, behavioral and kinematic diversity on prey-capture performance for different prey types.

The field of hydrodynamic forces in front of the fish's mouth results from the differential in speed and acceleration between the prey and the water around it, as well as from a gradient of flow across the prey (Wainwright and Day, 2007). Water speed and acceleration around the prey are driven by the following components: (1) the temporal pattern of flow at the mouth (increasing flow during the strike), (2) mouth displacement towards the prey (moving the mouth center, where flow is strong, closer to the prey), (3) the extent of mouth opening (increasing the reach of suction flows), and (4) the distance between the prey and the mouth center. The effects of the flow on the prey are also mediated by properties of the prey itself – its 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 (Holzman et al., 2008b; Skorzewski et al., 2010; Wainwright and Day, 2007). The consequences of all of these factors on prey capture performance, however, are often non-linear and dependent on the states of other variables. To account for this complexity, we designed SIFF as a tool for integrating these interdependent variables and quantifying the contribution of each factor to strike success.

Under SIFF, prey capture can be determined by the movement of the prey relative to the predator's mouth, which is also a function of the force exerted on the prey during the strike and its predator-avoidance strategy. For prey that cling to substrates (attached prey), capture success can be defined in terms of the suction forces exerted on the prey relative to its clinging force. For swimming and floating prey, capture can be defined as the moment when the distance

Table 1. Input variables used for suction-induced flow field (SIFF) and principal components analysis (PCA) on kinematic variables

SIFF	PCA
Vector of gape as a function of time (m)	Standard length (m)
Vector of flow speed as a function of time (m)	Time to peak gape (s)
Vector of mouth location as a function of time (m)	Peak gape diameter (m)
Prey size (length and diameter; m)	Protrusion distance (m)
Vector of escape or attachment force exerted by the prey as a function of time (N)	TTP mouth closing
	TTP hyoid depression
	TTP head elevation
	TTP jaw depression
	TTP maxillary rotation
	Maxillary rotation (deg)
	Head elevation (deg)
	Jaw rotation (deg)
	Hyoid depression (m)

TTP, time to peak event, relative to time to peak gape (in units of time to peak gape).

between the mouth and the prey becomes negative while the mouth is opened. That distance is a time-dependent function of the speed of mouth displacement towards the prey, the speed of prey movement and its direction (towards 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, variables easily quantified from high-speed videos of suction-feeding strikes. Prey movement is determined by the total force exerted on the prey (Wainwright and Day, 2007). In general, the total force exerted on the prey is the sum of five component forces: drag, acceleration reaction force, the force resulting from the pressure gradient across the prey, prey swimming forces and gravitational forces [the latter will be ignored through the current discussion because most aquatic organisms are approximately neutrally buoyant (Wainwright and Day, 2007)]. These combined forces are affected by the interaction of multiple mechanisms (Holzman et al., 2008b; Skorzewski et al., 2010; Wainwright and Day, 2007), which we integrated using SIFF. We applied SIFF to determine these forces and summed them over small increments of time and solved for the acceleration, speed and movement of the prey, and determined the strike's outcome – prey capture or escape.

SIFF inputs

As described above, the determinants of the forces exerted on prey are the speed and acceleration of water around the prey. Under a passive flow regime (i.e. flow into a wide orifice, a characteristic state in aquatic suction feeding), flow at the location of the prey can be inferred from the flow at the mouth center, given information on the size of the mouth and the distance between the mouth center and the prey (Day et al., 2005).

We used kinematic and morphological measurements to infer the magnitude and timing of peak flow speed in individual fish. We estimated peak flow speed for each individual as a function of its maximum capacity to generate suction pressure inside its buccal cavity, which is reflected by its suction index (SI), a combination of morphological variables previously shown to be directly proportional to suction pressure in centrarchids (Carroll et al., 2004; Holzman et al., 2008a). Details regarding the morphological measurements involved in determining SI for individual fish and the calculations for relating SI to flow speed appear in Holzman et al. (Holzman et al., 2011). Our use of SI to infer the magnitude of an individual fish's peak flow speed is based on hydrodynamic considerations [the Bernoulli principle (Muller et al., 1982; Van Wassenbergh et al., 2006; Vogel, 1994)] and empirical data (Higham

et al., 2006b; Holzman et al., 2008a), which indicate that suction pressure should be proportional to peak flow speed squared. We note that SIFF allows users to input measurements of flow speed obtained in ways other than the method described above, such as by direct measurement using flow visualization (Day et al., 2005; Higham et al., 2006a; Holzman et al., 2008a) or by inference based on the kinematics of buccal volume and gape expansion (Bishop et al., 2008; Muller et al., 1982; Van Wassenbergh and Aerts, 2009; Van Wassenbergh et al., 2006).

We measured gape size and mouth displacement speed for individual fish from 18 centrarchid species based on high-speed video (500 frames s⁻¹; NAC Memrecam Ci, Tokyo, Japan) of feeding strikes filmed in lateral view (Fig. 2A,B). For each species, we obtained video sequences from one to three individuals, and for each individual we sampled five strikes on live ghost shrimp under standardized experimental conditions (Holzman et al., 2011). Filming trials complied with all guidelines for the use and care of animals in research at the University of California, Davis.

We digitized landmarks on the fish and its prey to obtain the kinematic variables needed to parameterize the force model (Table 1). Frame-by-frame digitization was conducted using DLTdataviewer2 (Hedrick, 2008), a toolbox for automated kinematic analysis that runs in MATLAB (MathWorks, Natick, MA, USA), 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 that allowed us to calculate gape size, the location of the mouth's center, and the distance between the prey and the predator. From the mouth-opening phase of these digitized sequences, 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'). Following feeding trials, each fish was measured for standard length, a measure of fish body size. Species values for all kinematic variables were taken as the means of all sampled individuals weighted by the number of feeding trials.

We used strike kinematics as input for SIFF and estimated the temporal pattern of flow at the mouth by matching the time of flow initiation and peak flow speed to the gape cycle according to the stereotypical spatio-temporal pattern of flow observed for largemouth bass and bluegill sunfish (Higham et al., 2006a; Holzman

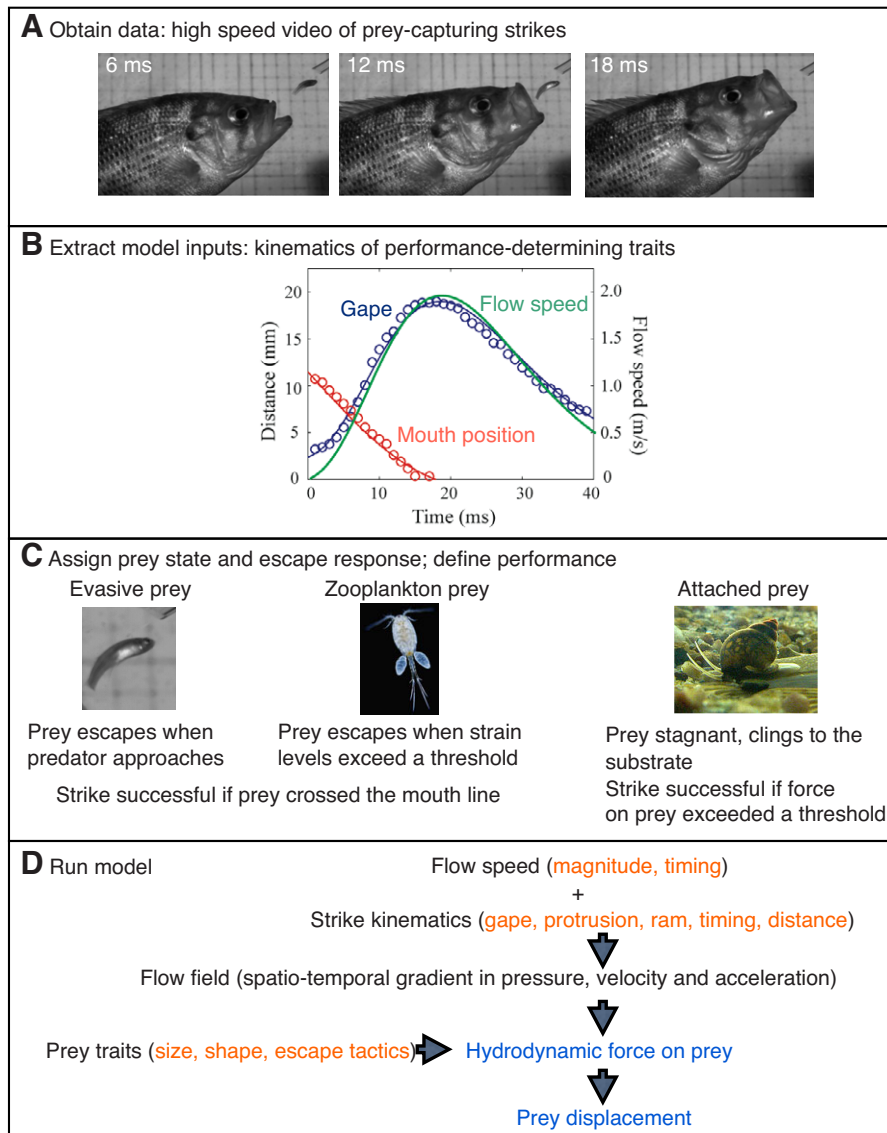


Fig. 2. Outline of data acquisition, SIFF inputs and output parameters. High-speed video of suction-feeding strikes (A) are recorded for fish, and digitized to extract the temporal pattern of mouth opening (blue circles in B), the temporal pattern of mouth displacement (red circles in B) and strike initiation distance (prey–mouth distance at time 0). To increase temporal resolution, continuous functions are fitted to observed mouth kinematics (blue and red solid lines in B). The temporal patterns of flow speed are estimated based on gape kinematics, and the peak magnitude of flow speed is estimated based on a morphological index that describes the force transmitted to expand the buccal cavity (green line in B). Thus, SIFF inputs are the solid lines in B, as well as parameters that represent prey characteristics (C), including the prey's response to the strike, prey dimensions and a set of hydrodynamic coefficients. SIFF then calculates the sum of escape and suction forces on the prey and solves for prey displacement (D). Performance is scored as peak force exerted by the suction flow on prey (for attached prey), the magnitude of escape force that evasive prey needs to recruit in order to escape, and the minimal sensitivity to strain that zooplankton prey needs to have in order to escape the strike.

et al., 2008a). We also estimated flow speeds and acceleration around the prey given the distance between the prey and the predator and the inferred flow field (Higham et al., 2006a; Holzman et al., 2008a; Muller et al., 1982; Van Wassenbergh and Aerts, 2009). We then fit continuous functions to gape size, the distance between the prey and predator, and the flow speed at the mouth with respect to time, which allowed us to calculate the flow speeds at the prey in intervals of 0.3 ms and derive accelerations at the frame of reference of the prey. These values were used, in turn, to infer forces exerted on the prey and its displacement towards or away from the mouth at each time step.

Simulated prey types

We ran SIFF to study performance with three general types of prey: attached, evasive and strain-sensitive, mobile zooplankton prey. These categories represent three broad, common trophic categories in fishes that pose different demands on the suction-feeding predator. We specified performance metrics for each prey type based on its characteristic functional demands. For attached prey, we determined for each predator species the peak force it can exert on attached prey. For escaping prey, we determined the maximal prey escape

force that the predator can overcome. Performance for strain-sensitive, mobile zooplankton prey was defined by the maximal prey sensitivity for which the predator could still capture the prey. Below we detail the parameters used for modeling the prey's response to the approaching fish for the three prey types (Fig. 2C,D).

In this study, attached prey adhered to the substrate with a force of 1.1×10^{-2} N (Holzman et al., 2008c; Wainwright and Day, 2007). Prey attached force was chosen such that capture rates were ~50% across all trials for all fish. Thus, we recorded prey capture if suction forces were higher than this force. Attached prey was modeled as a shrimp-like prey, 24 mm in length, 3 mm in maximum diameter.

To study performance on evasive prey, we allowed the prey to swim away from the predator as soon as the predator came within a threshold distance from the prey. We used MATLAB's built-in function (`fminbnd`) to optimize the predator–prey distance at which prey escape was initiated and yielded prey escape. We specified an escape trajectory oriented directly away from the fish. These escape vectors are consistent with optimal avoidance considerations (Weihs and Webb, 1984) and empirical observations of escaping shrimp (Arnott et al., 1999), copepods (Titelman, 2001) and minnows (Weihs and Webb, 1984). Escaping prey were also shrimp-like in

shape (24 mm in length, 3 mm in maximum diameter) and capture was noted when the distance between the mouth and the prey turned negative while the mouth was still open. We simulated strikes for 10 levels of escape force, ranging from 10^{-2} to 10^2 N [within the observed range for small evasive prey (Buskey et al., 2002; Lenz and Hartline, 1999)]. For each strike we determined the maximal escape force exerted by prey that still resulted in capture.

We modeled zooplankton prey to swim away from striking predators when water strain rates increased above a species-specific threshold, corresponding to flows that bend sensory hairs on the prey's antennae and elicit an escape response (Kiorboe and Visser, 1999). We simulated strikes for nine levels of this strain rate threshold (0.005, 0.01, 0.05, 0.1, 0.5, 1, 5, 10 and 100 s^{-1}), spanning the observed range for crustacean zooplankton (Kiorboe and Visser, 1999). We specified an escape trajectory oriented directly away from the fish, with an escape force of 6×10^{-4} N for a spherical prey 3 mm in diameter (Buskey et al., 2002; Lenz and Hartline, 1999). Prey capture was noted when the distance between the mouth and the prey turned negative while the mouth was still open. We then determined for each strike the maximal strain sensitivity exhibited by prey that resulted in capture.

Diet data

We compared rates of prey capture success inferred from SIFF with the proportion of attached, evasive and crustacean zooplankton prey found in the diet of centrarchid fishes. We quantitatively described the diets of the 18 centrarchid species based on a synthesis of published gut content analyses [for a full list see table 1 in Collar et al. (Collar et al., 2009)]. We combined data from studies that reported the contribution of taxonomic prey categories and averaged over variation in season, locality and size classes above adult body size. Stomach contents of fishes were quantified using three indices: percent numerical contribution (each prey category's percent of the total number of prey in the gut; %N), frequency of occurrence (the proportion of guts containing each prey category; FO) and percent volumetric contribution (each prey category's percent of the total volume of prey in the gut; %V). We retained only taxonomic prey categories that contributed more than 5% of the diet (according to any index) in at least one species. Despite our extensive literature search, none of the indices provided complete coverage of our 18 centrarchid species. Therefore, we combined information from the three indices by first standardizing the index values for each taxonomic category (i.e. transforming the dietary contribution for each taxonomic prey category to a standard normal distribution with a mean of 0 and standard deviation of 1). The taxonomic contribution for each species was then taken as the mean of the three standardized indices. This combined metric provided species' values for a suite of 19 prey categories that were then assigned to the functional groups considered in our simulation analysis: attached prey (Diptera, Hemiptera, Trichoptera, Ephemeroptera, Coleoptera, Odonata, Gastropoda and Bivalvia), evasive prey (fish, crayfish, decapod shrimp and Mysidacea) and crustacean zooplankton prey (Cladocera, Copepoda and Ostracoda). To evaluate the fit between species' feeding performance inferred by SIFF and observed diet patterns, we regressed species' suction-feeding performance for each prey type (e.g. force exerted on attached prey) on the contribution of each prey type to species' diets.

Principal components analysis

Principal components analysis (PCA) is one of the most commonly used methods of summarizing functional data in comparative analyses and is often used in feeding kinematic studies (Gibb and

Ferry-Graham, 2005; Gillis and Lauder, 1995; Wainwright and Lauder, 1986). We quantified a suite of 13 kinematic variables that are commonly measured in suction feeders (see Table 1) and performed a PCA on the correlation matrix of these variables following log transformation and size correction. Both our size correction and PCA accounted for phylogenetic relatedness using the method described by Revell (Revell, 2009). We then evaluated the strength of the relationship between kinematics and diet using a series of regression models in which the contribution of prey to species' diets were dependent variables and kinematic principal components (PC 1–4) were independent variables.

We then used the results of the PCA to identify the contribution of different traits to feeding performance. We used the loadings of the input traits on each PC axis, which reflect the contribution of the trait to the species score on each PC and the correlation coefficients between the PCs and the diet data. Statistically, these loadings are equivalent to the coefficients from a multiple regression model. We therefore quantified the contribution of each trait on performance as the sum of its loadings on kinematic PCs, weighted by the correlation coefficients for each PC (reflecting, for example, the variance in diet explained by each PC axis) such that:

$$E_{n,b} = \sum_{PC(i)} L_{PC(i)} \times Cor_{PC(i)-b}, \quad (1)$$

where E is the effect size of trait a on feeding performance on prey type b , L is the loading of trait a on $PC(i)$ and Cor is the correlation coefficient between the PC scores on $PC(i)$ and the diet index for prey b .

Statistical analysis

The non-independence of species due to shared evolutionary history needs to be addressed in comparative data sets. To test for phylogenetic signal in the independent and dependent variables involved in our regressions and correlations, we calculated Blomberg's K (Blomberg et al., 2003), which indicates the amount of covariance among species values relative to their expected covariance under a Brownian motion model and a phylogenetic tree. K -values of 1 reveal that species values covary as expected under Brownian motion and imply strong phylogenetic signal, whereas K -values near 0 indicate that species values do not covary in relation to their time of shared evolution. We evaluated whether significant phylogenetic signal was present in a variable (i.e. whether K differs from 0) using Blomberg et al.'s permutation test (Blomberg et al., 2003).

When phylogenetic signal was present, we used standardized phylogenetically independent contrasts in our regressions and correlations (Felsenstein, 1985). We used a species-level, time-calibrated, multi-locus molecular phylogeny for the Centrarchidae (Near et al., 2005) (Fig. 3) as the basis for calculating independent contrasts for all variables in the ape module of the statistical software R (R Development Core Team, 2009). Phylogenetic size correction (Revell, 2009) was performed on each SIFF-related variable prior to calculating contrasts.

To assess the contribution of each performance-determining variable to feeding performance for each prey type, we used a stepwise approach to build a multiple regression model, in which performance (e.g. force exerted on attached prey) was the dependent variable and putative functional components (gape size, suction distance, mouth displacement speed, time to peak gape, peak flow speed, peak flow acceleration, jaw protrusion distance and strike initiation distance) were independent variables. We used the backward–forward procedure that takes out and inserts independent variables through iterations and selected the best-fit model based on comparisons of Akaike's information criterion (AIC). Using the

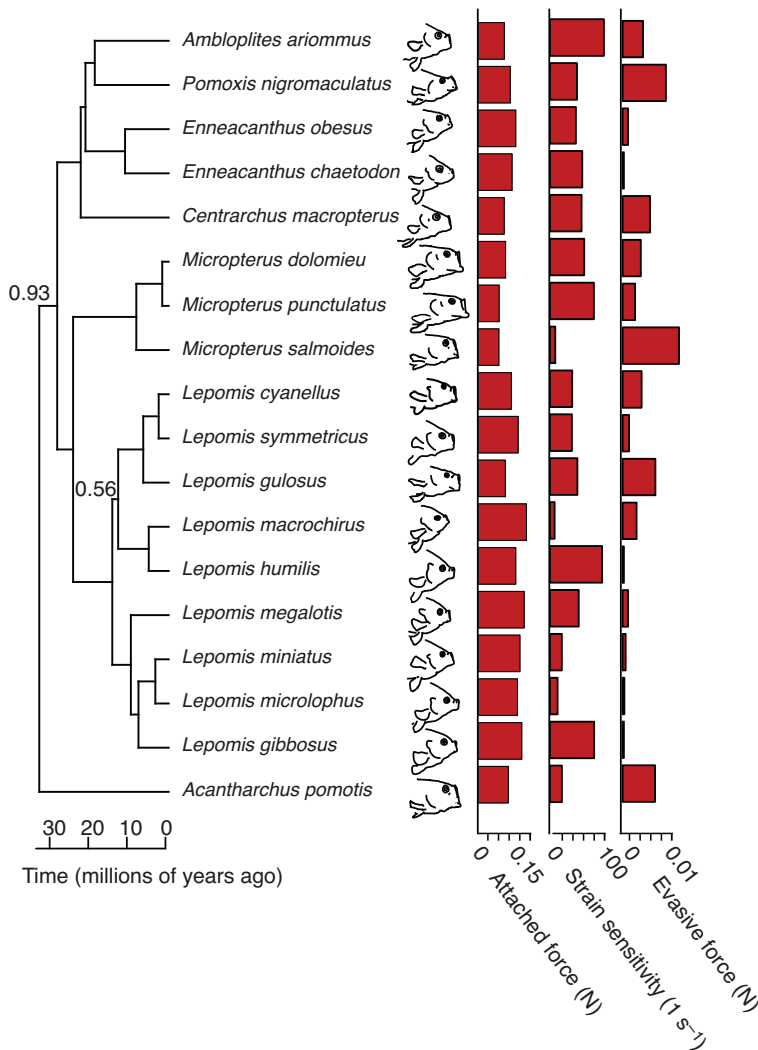


Fig. 3. Diversity of suction-feeding performance in Centrarchidae. Different demands imposed by different prey types (red bars; strike success on attached, evasive and zooplankton prey) lead to a multidimensional nature of suction-feeding performance, where success in feeding on one prey type (e.g. attached prey) does not necessarily predict success in feeding on other prey types (e.g. evasive prey). The scoring of strike success for each prey type is detailed in Fig. 2D. In the phylogenetic tree, nodes are supported by greater than 0.95 Bayesian posterior probabilities unless indicated otherwise.

preferred model, we calculated the relative effect sizes (Cohen's f^2) for each independent variable. Effect size is defined as the proportion of variance explained independently by a variable relative to the total variance explained by all variables in the model. Statistical analyses were performed using R, except for the calculation of Cohen's effect sizes, which were done by hand.

RESULTS

Correspondence between SIFF predictions and diet in centrarchids

Permutation tests involving Blomberg's K indicated that all performance-determining traits exhibited significant phylogenetic signal. We therefore fit correlation and regression models using phylogenetically independent contrasts (hereafter contrasts).

Overall, SIFF was a good predictor of diet evolution in Centrarchidae. We found a positive correlation between contrasts for attached prey in species' diets and the SIFF-inferred hydrodynamic force exerted on attached prey (major axis regression, $r=0.50$, $P<0.040$; Fig. 4A). Similarly, there was a positive correlation between contrasts for the evasive prey in the diet and inferred success rates of capture of evasive prey (major axis regression, $r=0.57$, $P<0.027$; Fig. 4B). There was no significant relationship between the contrasts for the dietary contribution of zooplankton prey and threshold escape strain rates of zooplankton prey (major axis regression, $r=-0.25$, $P>0.35$; Fig. 4C).

Traits that determine prey-capture performance – SIFF predictions

Stepwise multiple regression involving contrasts indicated that the significant performance-determining traits were different for the three prey types (Fig. 5A). Contrasts for the force exerted on attached prey were explained by contrasts for mouth displacement speed, time to peak gape, flow speed, jaw protrusion distance and strike initiation distance ($P<0.001$; Table 2). For evasive prey, contrasts for SIFF-inferred success rates were found to be a function of contrasts for gape size, time to peak gape, flow speed and strike initiation distance ($P<0.001$; Table 3). Lastly, contrasts for the ability to capture strain-sensitive prey were explained by contrasts for gape, mouth displacement speed, time to peak gape, flow speed and jaw protrusion distance ($P<0.001$; Table 4). Within the best-fitting multiple regression models for each prey type, effect sizes for the independent variables exhibited substantial variability [coefficient of variation (CV)=2.3, 3.04 and 3.5 for attached, evasive and zooplankton prey, respectively]. Traits that significantly contributed to more than one performance variable often had different effect sizes (Fig. 5A). For example, flow speed was the most important determinant for performance on attached prey, but played a minor role in determining performance on evasive prey (Fig. 5A). Similarly, time to peak gape was an important determinant of performance on zooplankton prey, but was much less important for attached prey. This variation in the functional basis of feeding performance is also supported by a mean correlation

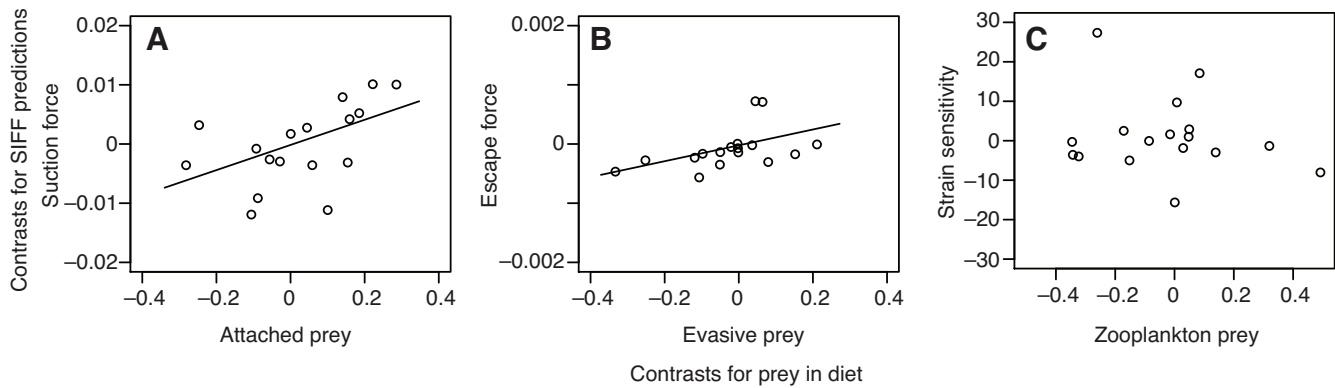


Fig. 4. Correspondence between diet data and SIFF estimates of suction performance on (A) attached, (B) evasive and (C) zooplankton prey. Data are presented as phylogenetically independent contrasts. Correlations between contrasts indicate that evolutionary increase in the force exerted on prey is correlated with an evolutionary increase in the abundance of attached prey in the diet (major axis regression, $r=0.50$, $P<0.040$), and that evolutionary increase in the SIFF-inferred ability to feed on evasive prey is correlated with an evolutionary increase in the abundance of such prey in the diet (major axis regression, $r=0.57$, $P<0.027$). The correspondence between the phylogenetic independent contrasts for the zooplankton prey diet index and the predators' ability to capture zooplankton prey was not significant ($r=-0.21$, $P>0.4$).

of $r=0.44$ between effect sizes for independent variables affecting different prey types.

Results from multiple regressions involving contrasts for diet variables as dependent variables (rather than SIFF-inferred performance) yielded fits (overall R^2 of 0.63, 0.87, 0.3 for attached, evasive and zooplankton prey, respectively) that were similar to those for SIFF-inferred performance. Effect sizes from multiple regressions were also highly correlated for attached and evasive prey ($r=0.99$ and 0.96 for the correlation between effect sizes in SIFF- and diet-inferred performance, respectively), though not for zooplankton ($r=-0.18$). In the discussion, we focus on coefficients from regressions involving estimates of performance derived from SIFF because of the strong mechanistic link between suction-feeding performance and its determinants.

In addition, we used SIFF estimates of performance to test for trade-offs between performance on attached, evasive and

zooplankton prey. We found that trade-offs were generally low and none of the pair-wise correlations were significant (attached–evasive performance trade-off: $r=-0.33$, $P>0.18$; zooplankton–evasive performance trade-off: $r=-0.47$, $P>0.053$; zooplankton–attached performance trade-off: $r=-0.34$, $P>0.17$; Fig. 6).

Correspondence between PCA of feeding kinematics and diet in centrarchids

The first four axes of the phylogenetically corrected PCA collectively explained approximately 85% of the variation in the kinematic data for Centrarchidae. PC 1 accounted for 38.0% of the variation and loaded strongly on standard length, time to peak gape, gape size, jaw protrusion distance, relative time to mouth closing and hyoid depression. PC 2 accounted for 19.6% of the variation and loaded strongly on relative time to mouth closing, relative time to peak head elevation, maximal jaw rotation, maximal head

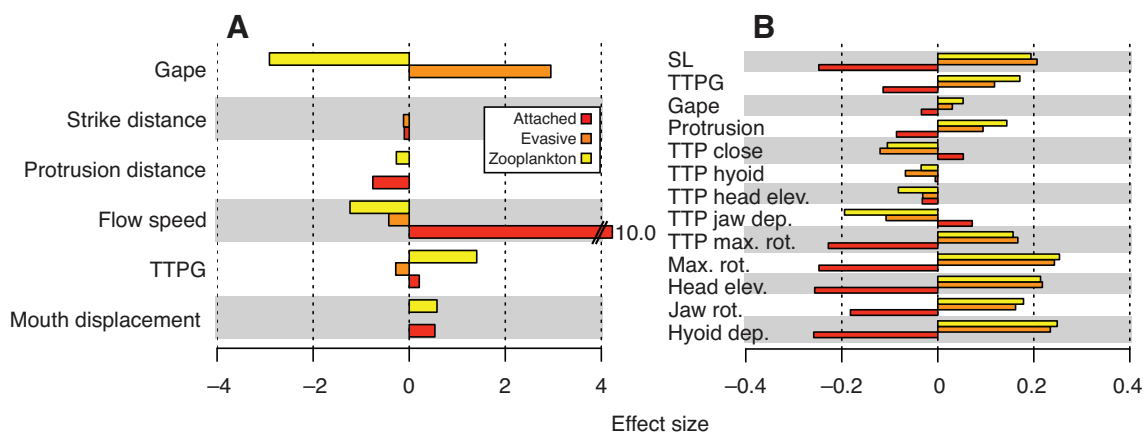


Fig. 5. Relative effect sizes for determinants of suction performance on attached (red bars), evasive (orange) and zooplankton prey (yellow) inferred from (A) SIFF and (B) PCA analysis. SIFF results indicated that different traits contributed to the evolution of performance, also indicated by the low correlation between absolute magnitude of effect sizes ($r=0.44$). In contrast, the PCA inference is that traits contributed similarly to the evolution of performance; correlations between absolute magnitude of effect sizes were strong ($r=0.96$), though the direction is reversed for some prey types, indicating a trade-off. Relative effect sizes for SIFF results are the proportion of variance explained by each independent variable, relative to the total variance explained by the multiple regression model (Cohen's f^2). The sign indicates whether the slope estimate is positive or negative. Only independent variables that had significant effect on suction performance are displayed. For the PCA analysis, effect sizes are the sum of the loadings on each PC, weighted by the proportion of variance explained by each PC and the correlation coefficient of that PC and each prey type. The x-axis in A is truncated at an effect size of 4. SL, standard length; TTPG, time to peak gape; TTP, time to peak event, relative to TTPG; dep., depression; elev., elevation; rot., rotation.

Table 2. Results from a stepwise multiple regression model testing the effects of dependent variables on attached prey capture, as predicted by SIFF

Variable	Slope (mean \pm s.e.m.)	t-ratio	P
Mouth displacement speed	9.22E-05 \pm 3.27E-05	2.817	0.015
Time to peak gape	1.14E+00 \pm 5.92E-01	1.928	0.077
Flow speed	7.53E-02 \pm 6.56E-03	11.478	<0.001
Protrusion distance	-1.86E-03 \pm 5.66E-04	-3.291	0.006
Strike initiation distance	-6.95E-04 \pm 4.55E-04	-1.527	0.152

Overall adj. $R^2=0.93$, $F_{5,12}=53.69$, $P<0.001$.

Table 3. Results from a stepwise multiple regression model testing the effects of dependent variables on evasive prey capture, as predicted by SIFF

Variable	Slope (mean \pm s.e.m.)	t-ratio	P
Gape	3.46E-04 \pm 5.33E-05	6.503	<0.001
Time to peak gape	-5.64E-02 \pm 2.54E-02	-2.22	0.044
Flow speed	-2.87E-03 \pm 1.09E-03	-2.639	0.020
Strike initiation distance	-6.93E-05 \pm 4.25E-05	-1.628	0.12

Overall adj. $R^2=0.80$, $F_{4,13}=17.8$, $P<0.001$.

Table 4. Results from a stepwise multiple regression model testing the effects of dependent variables on strain-sensitive prey capture, as predicted by SIFF

Variable	Slope (mean \pm s.e.m.)	t-ratio	P
Gape	-5.29 \pm 0.84	-6.232	<0.001
Mouth displacement speed	0.17 \pm 0.059	2.92	0.012
Time to peak gape	4272 \pm 972	4.392	<0.001
Flow speed	-66.5 \pm 16.1	-4.127	0.001
Protrusion distance	-3.0 \pm 1.41	-2.118	0.05

Overall adj. $R^2=0.81$, $F_{5,12}=15.93$, $P<0.001$.

elevation and jaw rotation speed. PCs 3 and 4 explained 17.6 and 9.4% of the variation, respectively, and both loaded heavily on relative time to peak hyoid depression, relative time to peak jaw depression, relative time to peak maxillary rotation and (PC3 only) relative time to peak head elevation. However, the distribution of species in the kinematic space was only a moderate predictor of diet (Fig. 7, Table 5). PCs 1 and 2 had moderate to low correlations with diet contrasts ($|r|$ ranging from 0.45 to 0.23), which were marginally non-significant ($P=0.06$; without a Bonferonni correction that takes into account the multiple tests performed on the four axes). PCs 3 and 4 had much lower correlations with diet contrasts ($|r|$ ranging from 0.36 to 0.06), and these correlations were all non-significant ($P>0.15$).

Traits that determine prey-capture performance – PCA predictions

We used the loadings of kinematic traits on each PC axis and the correlation between each PC axis and diet to identify kinematic traits that contribute to performance (see Eqn 1). In contrast to the SIFF inference, this analysis indicated that all traits contributed similarly to the evolution of performance. In general, effect sizes for the kinematic traits exhibited moderate variability (CV=1.0, 1.4, and 1.6 for attached, evasive and zooplankton prey, respectively). Moreover, traits had similar effects on performance with different prey types. For example, maxillary rotation and head elevation had similar effects on evasive and zooplankton prey (Fig. 5B). Those two traits had similar effect-size magnitudes for attached prey in

the diet, but the effect direction was reversed. This similarity in magnitude but opposite direction of effect size indicates a strong trade-off and was reflected by the tight correlations between absolute magnitude of effect sizes for feeding on attached, evasive and zooplankton prey (mean $r=0.96$; Fig. 5B).

DISCUSSION

Suction-feeding performance in fishes is often examined along a single axis, highlighting contrasts between good and poor suction-feeding species. This tendency emerges from studies that have attempted to distill suction-feeding performance to statistically convenient individual performance traits such as buccal pressure (Carroll et al., 2004), ram-suction index (Nemeth, 1997), the flow of water in front of the mouth (Higham et al., 2006a) or the force exerted on attached prey (Holzman et al., 2008b). Although each of these metrics captures some aspect of diversity of aquatic feeding, any one reduces the dimensionality within which suction-feeding performance is viewed. In reality, prey-capture performance as it relates to suction feeding is a function of many factors, including the ability to generate suction pressure, the predator's approach strategy and the prey's response to the strike.

Our SIFF results reinforce the intuition that different prey types place different demands on the suction feeder. The multiple regression analysis (Tables 2–4) indicated that traits had quantitatively different effects on attached, elusive and zooplankton prey; for example, traits that contributed much to feeding on attached prey were not as important for feeding on evasive prey (Fig. 5A).

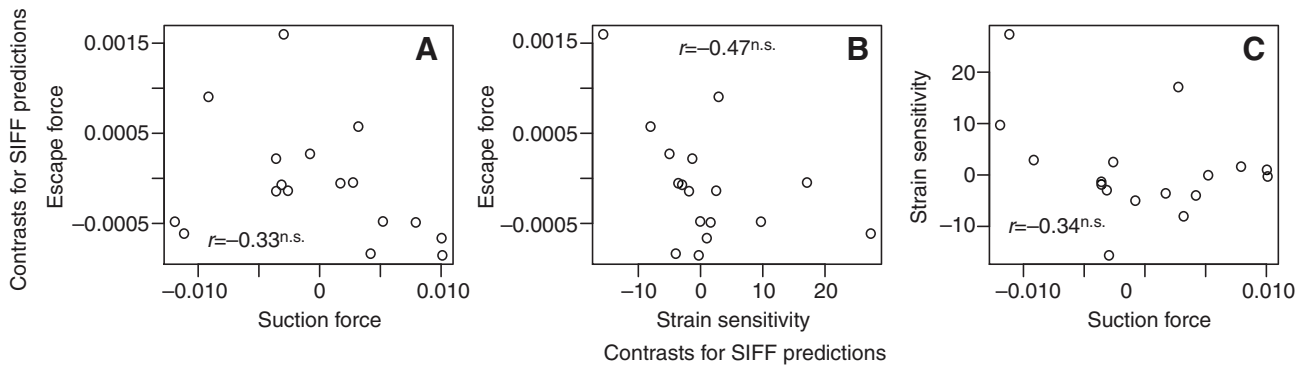


Fig. 6. Suction performances predicted from SIFF showed little evidence of trade-offs between feeding performance on (A) attached, (B) evasive and (C) zooplankton prey. We attribute this lack of trade-offs to the fact that different suites of traits determine performance on each prey type. n.s., not significant.

This suggests a certain amount of functional independence between feeding on different prey types, a pattern that is supported by the weak trade-offs between the three performance traits across centrarchids. Although we focused on major functional categories of centrarchid prey, this approach could easily be extended to consider additional prey types or individual prey species.

SIFF versus PCA in accounting for suction-feeding performance

SIFF output and the PCA showed different abilities to account for dietary variation among centrarchids. First, SIFF-inferred performance correlated more strongly with diet, specifically for attached and evasive prey. Second, SIFF revealed that different traits have differential effects in determining performance on prey types, whereas the PCA revealed that traits have similar effects on attached, evasive and zooplankton prey. Our approach with SIFF

was to use multiple regression models to estimate the effect of variables on feeding performance (Tables 2–4). To identify traits that contribute to performance in the PCA, we used the loadings of the original kinematic variables and weighted them by the amount of variance in diet explained by each PC. We found correlations between PC 1 and the abundance of attached, evasive and zooplankton prey were similar in magnitude (Table 5), suggesting that variables loading heavily on PC 1 contribute similarly to performance on each of the three prey types. This is a fundamentally different result than the one provided by the SIFF results. We interpret this discrepancy as a consequence of applying mechanistic versus statistical models.

The multivariate exploratory statistics commonly used to study fish feeding kinematics (such as PCA, multidimensional scaling and canonical correlations) are designed to identify the major axes of variation in a data set containing many variables. These techniques

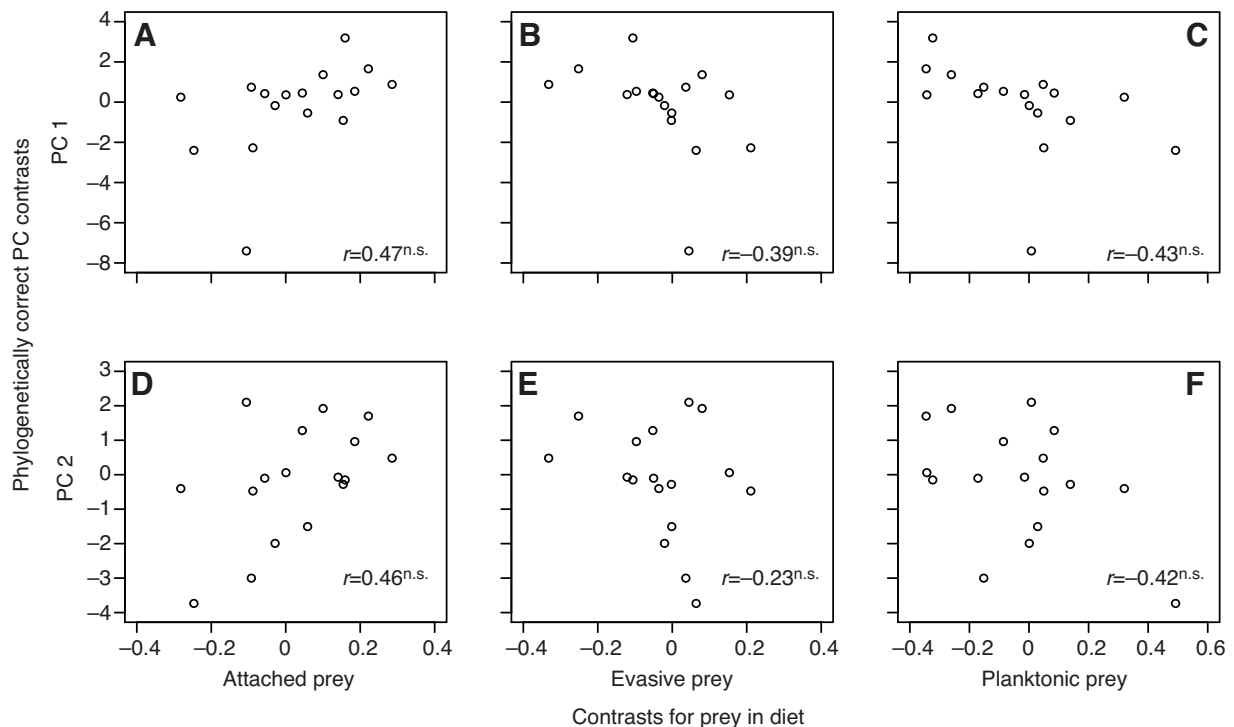


Fig. 7. Correspondence between contrasts for prey types in centrarchid diets and contrasts for PCs 1 and 2. The correlations between these PCs (for loadings, see Table 5) and abundance of prey were not significant.

Table 5. Summary of major axis regression results between scores on PC 1–4 and the proportion of attached and evasive prey in the diet of 18 centrarchid species

PC	% Variance explained	Attached		Evasive		Zooplankton	
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
1	38.0	0.45	0.068	−0.39	0.11	−0.43	0.08
2	19.6	0.46	0.06	−0.23	0.36	−0.42	0.08
3	17.9	0.02	0.9	0.12	0.64	0.35	0.15
4	9.4	0.3	0.23	−0.36	0.15	0.13	0.61

Data for the analysis are phylogenetically independent contrasts (*F*-ratios are for 1,16 degrees of freedom) of PC scores.

reduce dimensionality by accounting for covariation in the data and returning new axes describing variation that is shared among variables. The output of such analyses includes a list of scores, indicating the distribution of points along the new set of axes. Effectively, closer points indicate similarity and further points indicate larger dissimilarity, or variance. The variables that contribute most to variance along the new axes are also commonly identified. These properties seem well suited to the analysis of kinematic data that often contain many correlated variables. The core assumption that follows the implementation of such techniques to study feeding performance is that the overall kinematic similarity is a good indication of the overall performance similarity. Our results, however, reveal that species scores on PCs 1–4 were weakly correlated with the proportion of benthic or evasive prey in the diets of our 18 species. We conclude that, at least for centrarchids, the overall kinematic similarity is a poor indication of the overall performance similarity.

We suggest that this discordance is due to the multitude of mechanisms that contribute to feeding performance. Consider, for example, a comparison between two strikes: the first has low acceleration of the suction flow but two other independent mechanisms, fast jaw protrusion and accurate timing, enhance the acceleration on the prey; the second strike has high flow acceleration and no effect of the independent mechanisms. In the kinematic space, these strikes will be disparate; however, in performance space they could be similar if jaw protrusion and timing compensate for the reduced acceleration. Additionally, the assumption that the overall kinematic and performance similarity are linked could be invalidated because the effects of kinematic variables may be non-linear, non-monotonic and context dependent. For example, if strike starting distance has a small effect on capture performance between 1 and 5 mm and a large effect between 5 and 10 mm, strikes with a start distance of 3 and 5 mm will be similar in both kinematic and performance space (all else being equal) but strikes with a start distance of 7 and 5 mm will be more similar in kinematics than in performance. If the effect of variables on performance is non-monotonic, e.g. an increase in strike distance above 15 mm will reduce strike success, a pair of strikes with striking distances of 5 and 7 mm will have the same kinematic similarity as a pair with 16 and 18 mm, but the effects on performance are reversed. Lastly, if strike initiation distance has a small effect on performance, strikes can be disparate in kinematic space but similar in performance space. In all those cases, the kinematic space will not map directly to the performance space.

Independence in the determinants of performance on different prey

A situation where different functional components underlie different performance traits can lead to considerable independence in the evolution of performance traits. Holzman et al. (Holzman et al.,

2011) showed that having multiple traits contribute to performance can weaken trade-offs between those performance axes. We similarly demonstrate low trade-offs in the functional demands imposed by the three prey types, as inferred by SIFF. These low functional trade-offs are also manifested as weak trade-offs between the abundance of three prey types in centrarchid diets. For example, SIFF predicts that gape size has opposite effects on the ability to capture evasive and zooplankton prey, perhaps because large gape extends the reach of suction flow (Holzman et al., 2008a) whereas small mouths reduce the spatial extent of hydrodynamic ‘noise’ produced by the suction flow that may alert strain sensitive prey (Holzman and Wainwright, 2009). However, this trade-off can be mitigated by evolutionary changes to any other trait that affect only one of the two performance traits. According to our inference (Fig. 5), for example, the degree of jaw protrusion has a large effect on the ability to capture zooplankton prey and can be extended in response to selection to enhance that performance. Thus, the combination of traits such as a large mouth and extended jaw protrusion [as seen in the cichlids *Petenia splendida*, *Caquetaia kraussii* and *Caquetaia myersi* (Hulsey et al., 2010)] may be viewed as an adaptation to efficiently capture two prey types that place opposing demands on the cranial structure, with fast jaw protrusion evolving to mitigate detrimental effects of large gape (needed to capture evasive prey) on the ability to capture zooplankton prey.

The functional basis of suction-feeding performance

Our study found significant correlations between SIFF predictions and the dietary contribution of attached and evasive prey, allowing us to make predictions about the consequences of the morphological and kinematic specializations exhibited in centrarchids. These predictions can be cautiously generalized to the broader range of suction-feeding fishes and thus SIFF can serve as the basis for generating new hypotheses on the functional basis of aquatic suction-feeding performance.

The abundance of evasive prey in the diets of centrarchids (mainly fish, shrimp, crayfish and mysids) was correlated with SIFF predictions to determine the prey’s escape force needed to overcome the predator’s strike. SIFF results indicate that gape size is mechanistically involved in determining the success rates of capturing evasive prey, perhaps through its effect on the reach of suction flow (Table 3). This mechanism is different than the commonly held hypothesis that a large mouth allows greater dependence on a less-accurate ram strategy, and reduced reliance on suction (Norton and Brainerd, 1993). The correlation between large gape size and predation on large, evasive prey has long been recognized in several groups of fishes (Collar et al., 2009; Keast, 1985; Wainwright and Richard, 1995b; Werner, 1977; Westneat, 1995), though the consequences of gape for extending the spatial reach of the flow and its potential influence on evasive prey capture have only recently been recognized (Day et al., 2005; Holzman et

al., 2008a). However, other determinants of suction performance emerge as relevant mechanisms that enhance feeding success on evasive prey (Fig. 5; Table 3). SIFF also predicts that strikes with shorter time to peak gape (faster strikes) and shorter strike initiation distance should also be favored when striking on evasive prey, but that fast flow is not strongly associated with evasive prey capture (Fig. 5; Table 3).

The abundance of benthic prey in the diets of Centrarchidae was correlated with the calculated force exerted on attached prey and the ability to dislodge attached prey by means of suction (Holzman et al., 2007). In general, the mechanisms that determine feeding success on benthic prey have been less clear. One recent hypothesis based on hydrodynamic considerations suggested that the capacity to generate large suction pressure and high-velocity and high-acceleration flow is beneficial to capturing attached prey because water moving past clinging prey will exert large drag and acceleration reaction forces (Holzman et al., 2008b; Wainwright and Day, 2007). This hypothesis is clearly supported by the dominance of acceleration-associated determinants of performance on attached prey. Faster mouth displacement speed and faster flow speeds are both associated with higher acceleration at the prey. In addition, short protrusion and strike initiation distance were correlated with higher force, perhaps because such strikes bring the prey close to the mouth where strong flows and steep flow gradients exist. The effect of time to peak gape was the opposite of what we expected, though effect size was small for this variable (Fig. 5).

We found that SIFF-inferred performance on zooplankton prey depended on small gape, likely because a small mouth generates large pressure gradient forces and limits the hydrodynamic disturbance close to the mouth. In addition, fast mouth displacement acts to surprise the prey. But SIFF-estimated performance failed to explain the occurrence of zooplankton prey in centrarchid diets. This could be attributed to SIFF parameterization, which may not accurately account for prey behavior. It could also be that, in Centrarchidae, other factors not included in the SIFF model, such as visual acuity, are crucial to the ability to feed on zooplankton prey. We note, however, that centrarchids are probably not the ideal group to test the ability of SIFF-inferred performance to predict the dietary contribution of zooplankton prey. Of the three prey categories we considered, zooplankton prey were the least abundant prey in all three metrics of prey abundance (mean values of 7.3, 3.8 and 19.9% for FO, %V and %N, respectively). In fact, more than half the species had no zooplankton prey in their guts for two of the three diet metrics (FO and %V). We speculate that centrarchids may take advantage of zooplankton prey when they are available, though species may not be well adapted to capturing them. However, it might also be that this prey category encompasses much higher diversity in escape strategies and forces than accounted for in our model, and our treatment of this group as functionally uniform could be responsible for the poor match between SIFF-inferred performance and zooplankton abundance in centrarchid diets.

Previous attempts to identify the biomechanical and morphological contribution to diet have mostly taken a statistical approach, focusing on correlations between morphological traits and diet (Costa, 2009; Hulsey and Garcia De Leon, 2005; Keast, 1985; Wainwright and Richard, 1995a; Werner, 1977). Another study (Sibbing and Nagelkerke, 2000) attempted to predict diet-based morphology using biomechanically informed rankings of the importance of several morphological traits to performance on multiple prey types. Here we use SIFF as a modeling tool that entails no assumptions on the role of traits on performance. Rather, SIFF uses hydrodynamic principles to predict performance on prey

during suction-feeding strikes. An earlier implementation of a similar approach (Van Leeuwen and Muller, 1984) was restricted to the case of free-floating, neutrally buoyant prey that behave as parcels of water. Wainwright and Day (Wainwright and Day, 2007) extended the framework to deal with heavy, swimming and attached prey. They proposed that, because of the radial symmetry of the suction flows, a one-dimensional (1-D) model of the flow-prey interaction (where only the distance between the prey and predator is input into the model) would suffice to understand the mechanisms that determine performance. Their model was empirically validated for large attached prey (Holzman et al., 2008b; Holzman et al., 2007) and both timing and magnitude of the observed forces were found to fit well to those measured using a force transducer. Van Wassenbergh and Aerts (Van Wassenbergh and Aerts, 2009) and Skorzewski et al. (Skorzewski et al., 2010) used two- and three-dimensional (3-D) computational fluid dynamic modeling and found general agreement with the 1-D model results. The 1-D and 3-D models rely on the sum of forces that are exerted on the prey to predict its movement and the outcome of the predator-prey interaction. The 1-D model is less computationally intensive and is accessible for less-technical users. The 3-D model is, in principal, a more accurate model, and enables, for example, the estimation of the effects of prey shape on feeding success (Van Wassenbergh and Aerts, 2009).

Prognosis for the use of SIFF to study suction-feeding performance

Our results support the use of SIFF to integrate the effects of kinematic and morphological variation on prey-capture performance. User-friendly MATLAB code that implements SIFF for attached, evasive and zooplankton prey as a means for studying the mechanistic basis of suction feeding and the diversity of suction-feeding performance across fishes is available *via* our website (http://www.iui-eilat.ac.il/faculty/roi_SIFF/roi_SIFF.aspx and http://www.eve.ucdavis.edu/~wainwrightlab/SIFF_web_page/SIFFnew.html). We suggest that studying the mechanistic basis of suction feeding with SIFF can be done by sequentially changing each input parameter (Holzman et al., 2008b) to monitor its effect on performance. Alternatively, the mechanistic basis of performance can be studied by running SIFF with parameter values obtained from different species (as done here) and teasing out the independent effects of the parameters using a statistical model. The latter approach can also be used to understand the role of kinematic and morphological traits in explaining diversity in performance. Clearly, it would be valuable to test the utility of SIFF for gaining insights into other radiations.

Obtaining measurements for SIFF's input parameters is not fundamentally different than measuring kinematic variables for multivariate statistical analysis, and requires only additional information on the speed of flow in front of the mouth. This can be measured from particle image velocimetry analysis (Higham et al., 2006a; Holzman et al., 2008a), based on either the expansion of the buccal cavity (Bishop et al., 2008; Van Wassenbergh et al., 2006) or morphological and kinematic proxies (Holzman et al., 2011). In this study we estimated peak flow speed from the SI model (Carroll et al., 2004), which entails several assumptions, including that the shape and temporal patterns of buccal expansion are conserved among species. At least within centrarchids, these assumptions seem to hold. The time to peak gape was highly correlated with the time to peak hyoid depression ($r=0.87$) and head elevation ($r=0.93$). The magnitude of hyoid movement was also tightly correlated with gape movement ($r=0.94$). Therefore, expansion dynamics seem to be conserved within centrarchids, and buccal

expansion can be predicted based on changes in gape. Nevertheless, the use of the SI probably underestimates the true diversity of peak flow speeds in centrarchids and likely reduces the accuracy of our predictions. We emphasize that this effect is a limitation not of SIFF, but rather in our estimates of one of SIFF's input parameters – flow speed at the mouth.

One possible limitation of our modeling approach is that we used kinematics recorded from feeding strikes on a standardized prey type (a shrimp) as input for SIFF's performance predictions on three different prey types. Individual fish are known to change their strike kinematics with prey type, modifying gape size, cranial elevation and time to peak gape (Wainwright et al., 2001; Wainwright et al., 2007), and this variation likely increases performance on different prey. We did not include this variation as input in SIFF because obtaining high-speed videos of strikes on multiple prey types for multiple individuals from each of 18 species would be potentially prohibitive. This detailed kinematic information would likely increase the accuracy of SIFF's performance estimates, but we accounted for the potential loss of accuracy by optimizing strike initiation distance (separately for each prey type) to achieve maximal probability of success for each strike. In addition, we found that additional kinematic data for different prey types may be unnecessary because SIFF-inferred performance agrees well with the diet data, thus validating our modeling approach despite its assumptions.

SIFF is designed only to predict suction-feeding performance and cannot take into account other strategies of prey capture. For example, some fish use biting to capture prey (Ferry-Graham et al., 2002; Ferry-Graham et al., 2001; Mehta and Wainwright, 2007a; Mehta and Wainwright, 2007b). If the role of suction feeding in prey capture is lessened in favor of other mechanisms such as biting, SIFF predictions may be biased. Adaptations for biting could potentially sacrifice suction production if hypertrophied biting muscles constrain buccal cavity size. SIFF estimates for feeding performance based on considerations of suction-induced flow would likely be low in a biting species, even though it may have high success rates of capture by biting. Studies on biting in catfish, however, reveal no such trade-off between biting and suction ability (Van Wassenbergh et al., 2007), and perhaps little bias would result for these species.

SIFF provides an opportunity to incorporate mechanistic biomechanical models into ecological foraging theory. For example, SIFF is a biomechanical model that predicts performance for different (observed or simulated) predator and prey combinations. These performance estimates can then be applied to evaluate the costs associated with feeding on different prey types (as handling time or risk of strike failure), to rank prey preference, and ultimately predict prey switching, patterns of selectivity and the outcome of inter- and intra-specific competition. Using mechanistic models to study ecological and evolutionary problems is not a new approach (Daniel and Meyhofer, 1989; Denny et al., 1985; McHenry and Patek, 2004). In fact, mechanistic models for studying suction-feeding performance and the evolution of diet have previously focused on the functional architecture of the musculo-skeletal system (Alfaro et al., 2006; Bellwood et al., 2006; Ferry-Graham et al., 2001; Liem, 1984). In contrast, SIFF combines the effects of morphology and kinematics to make quantitative predictions about properties of the suction-induced force and the resulting effects on prey in suction-feeding fishes.

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