Kinematic integration during prey capture varies among individuals but not ecological contexts in bluegill sunfish, *Lepomis macrochirus* (Perciformes: Centrarchidae)

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The general ability of components of an organism to work together to achieve a common goal has been termed integration and is often studied empirically by deconstructing organisms into component parts and quantifying covariation between them. Kinematic traits describing movement are useful for allowing organisms to respond to ecological contexts that vary over short time spans (milliseconds, minutes, etc.). Integration of these traits can contribute to the maintenance of the function of the whole organism, but it is unclear how modulation of component kinematic traits affects their integration. We examined the integration of swimming and feeding during capture of alternative prey types in bluegill sunfish (*Lepomis macrochirus*). Despite the expected modulation of kinematics, integration within individuals was inflexible across prey types, suggesting functional redundancy for solving a broad constraint. However, integration was variable among individuals, suggesting that individuals vary in their solutions for achieving whole-organism function and that this solution acts as a 'top-down' regulator of component traits, which provides insight into why kinematic variation is observed. Additionally, variation in kinematic integration among individuals could serve as an understudied target of environmental selection on prey capture, which is a necessary first step towards the observed divergence in integration among populations and species.

ADDITIONAL KEYWORDS: kinematics – individual variation – integration – prey capture – swimming – suction.

INTRODUCTION

Organisms are composites of hierarchically arranged structural and functional components, and complex traits at the whole-organism level emerge from the coordinated use of these components in space or time to generate a shared outcome. This emergent outcome has been generally termed integration (Bayliss, 1921; Olson & Miller, 1958; Gould & Lewontin, 1979; Zweers, 1979; Seaborg, 1999; Pigliucci, 2003; Korn, 2005), and is detected empirically as biological covariation among components (Pigliucci, 2003). Examination of organisms using this holistic approach can lead to additional insight into the success and persistence in the environment that would not be possible by studying each component in isolation (Olson & Miller, 1958; Zweers, 1979). For example, because interdependence is necessary to maintain function, traits may be limited in the way they can adapt in response to new functional demands. Inseparable links between components can constrain the ability for any one component to be modified (Goswami *et al.*, 2016; Haber, 2016), but suites of traits could also be modified together to facilitate adaptation in multiple components simultaneously (Badyaev & Foresman, 2000; Peres-Neto & Magnan, 2004; Hu *et al.*, 2007; Parsons *et al.*, 2018). Alternatively, novel functions may be possible only when integration is relaxed and links are broken (Hernandez & Cohen, 2019). These examples reflect changes on long temporal scales across generations, but it is less clear how these potential constraints apply when component traits are flexible on short time scales, within the lifetime of the individual.

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In contrast to morphological traits, which were examined in the examples above, kinematic traits describing movement are useful for quantifying how organisms use structural components on short time scales, ranging from milliseconds to minutes. Given that motor output can be influenced by behavioural regulation, this introduces a degree of flexibility in traits that cannot be observed for morphological traits. For example, in fishes, success in escaping a predator is dependent not only on achieving high velocity, but also on the behaviourally regulated timing and rate at which velocity is achieved (Walker *et al.*, 2005). This kinematic response of the locomotor system can also be variable from one encounter to the next (Domenici, 2010), demonstrating flexibility across contexts (Wainwright *et al.*, 2008). However, like morphological traits, kinematic traits can be integrated across systems that generate different types of functional responses, probably through coordination facilitated by neural control (Olsen *et al.*, 2019). For example, locomotor kinematics can be integrated with sensory systems (Rice, 2008; Falk *et al.*, 2014, 2015; Mandecki & Domenici, 2015), ventilation (Boggs, 2002; Tytell & Alexander, 2007) or feeding (Higham, 2007a; McElroy *et al.*, 2008; McBrayer & Wylie, 2009; Montuelle *et al.*, 2012b; Larouche *et al.*, 2015), suggesting that whole-organism integration across systems that can accomplish different functions may be readily apparent in organisms. Furthermore, if kinematic traits require integration in certain contexts, behavioural flexibility may impose limitations on how systems can be integrated.

However, it is unclear how behavioural modulation, or the often-observed change in kinematic outcomes in response to environmental context (Liem, 1978, 1979; Deban, 1997; Domenici, 2010; Van Wassenbergh & De Rechter, 2011; Gardiner & Motta, 2012; Foster & Higham, 2014; Seamone *et al.*, 2014), might be related to integration across kinematic traits (Fig. 1). If differences among contexts do not require a change in kinematic response or the need for higher-level function constrains kinematics, then modulation of component traits may not occur (Fig. 1A–C). In the absence of modulated kinematics, three outcomes for integration are possible: integration may be inflexible across contexts (Fig. 1A) or the covariation among kinematic traits may be regulated behaviourally such that it can vary in degree (Fig. 1B) or presence (Fig. 1C) depending on a desired whole-organism outcome. In this case, flexibility of integration with context may not be possible or may be achieved through modulation of integration only.

Alternatively, if differences among contexts are great enough to require modulation of kinematics or the need for a higher-level function directs changes in kinematics, modulation of kinematics will probably be apparent (Fig. 1D–F). In the presence of modulated kinematics, an additional three outcomes for integration are possible: integration may be constrained and similar across contexts (Fig. 1D) or integration could vary in degree (Fig. 1E) or presence (Fig. 1F) across contexts. In this case, flexibility across contexts may be achieved through modulation of kinematic traits only, or through modulation of both kinematics and their integration. Modulation of integration could be attributable to weakening or a breakdown of integration as a result of kinematic modulation, or integration might be less necessary and therefore permit modulation of kinematics. If flexibility of integration is supported, it might provide a mechanism for fine-tuning whole-organism outcomes on short temporal scales that could be advantageous in heterogeneous environments (Nemeth, 1997a, b).

Fishes are ideal for examining kinematics and its integration across functional systems because spatial constraints on suction (Ferry-Graham *et al.*, 2003; Day *et al.*, 2005) require that feeding is coordinated temporally and spatially with the locomotor system to approach prey before and during capture (van Leeuwen & Muller, 1984; Higham, 2007a; Ferry *et al.*, 2015; Longo *et al.*, 2015). Additionally, the chance of successfully capturing prey is maximized when predators position the suction volume accurately relative to the prey (Holzman *et al.*, 2008b; Kane & Higham, 2014). As a result of these factors, approach speed (also referred to as ram speed) and mouth size often covary in fishes such that higher ram strategies are coupled with a larger mouth aperture that increases volume intake but compromises suction force (Higham, 2007b; Kane & Higham, 2015; Kane *et al.*, 2019a, b). Although it is well known that predators can modulate both approach and capture kinematics (Norton, 1991; Anderson, 1993; Norton & Brainerd, 1993; Lemell & Weisgram, 1996; Nemeth, 1997a; Ferry-Graham *et al.*, 2001; Matott *et al.*, 2005; Van Wassenbergh *et al.*, 2006; Van Wassenbergh & De Rechter, 2011; Gardiner & Motta, 2012; Kane & Higham, 2014), it remains unclear how this modulation affects the integration of swimming and feeding movements during prey capture.

To determine how modulation of kinematic movements can impact whole-organism function through integration, we analyse suction feeding capture attempts on functionally divergent prey types in bluegill sunfish (*Lepomis macrochirus*). Bluegill sunfish have become a model of locomotor and suction feeding behaviours (Lauder & Lanyon, 1980; Day *et al.*, 2005; Holzman *et al.*, 2008a; Flammang & Lauder, 2009; Xiong & Lauder, 2014; Camp *et al.*, 2018) and show a wide range in their ability and propensity to capture various prey types (Crowder & Cooper, 1982; Mittelbach, 1983; Higham *et al.*, 2005; Carroll & Wainwright, 2009; Holzman *et al.*, 2012; Kane &
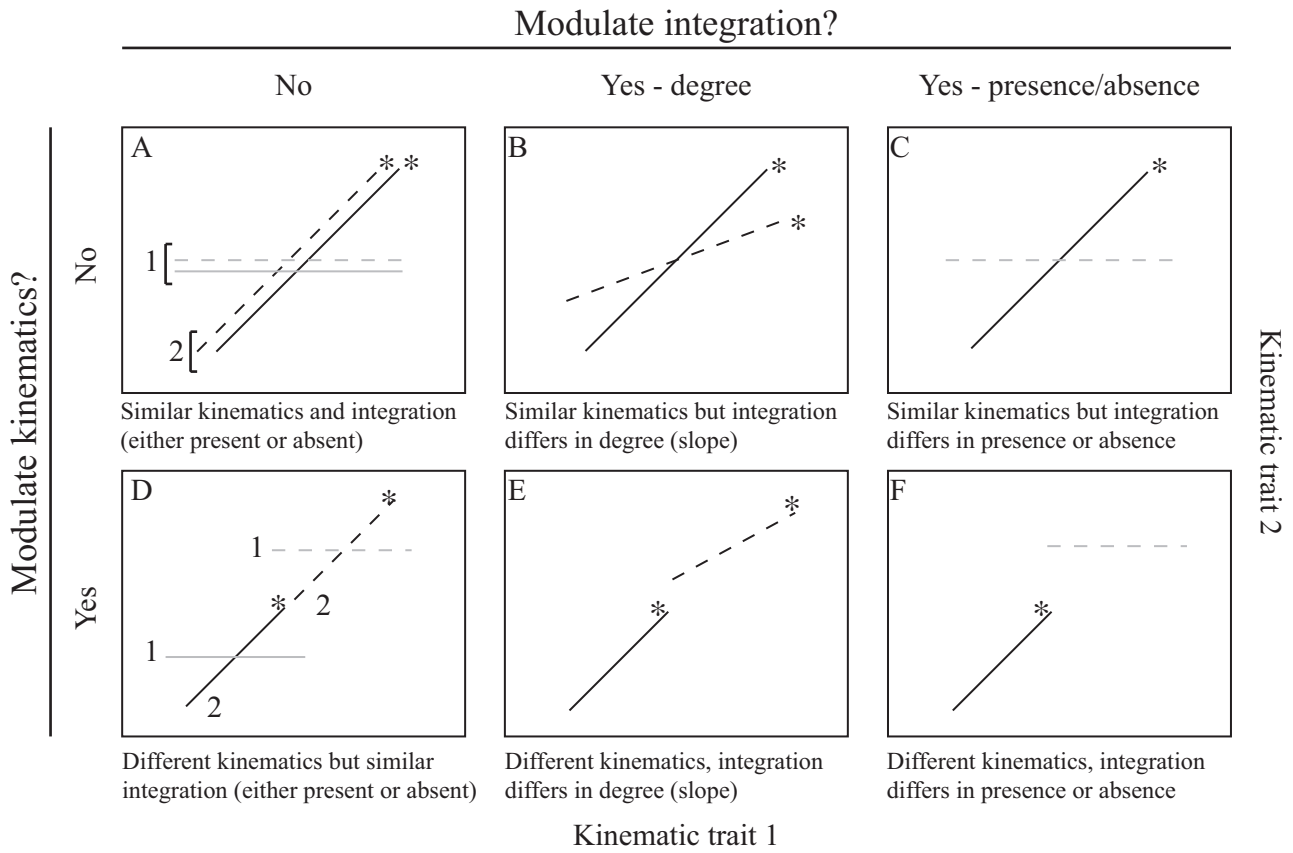
Modulate integration?

Figure 1. Theoretical outcomes comparing the possibilities for modulation of kinematic traits (rows) with the modulation of their integration (columns) across contexts such as prey type (continuous vs. dashed lines). Observations could represent individual outcomes or population-level outcomes if all individuals respond in a similar manner. Regression analyses of kinematic trait 2 against kinematic trait 1 are used to indicate covariance. Asterisks (*) and black lines indicate integration as identified by a slope significantly different from zero, whereas grey lines indicate no relationship (integration is absent). Component kinematic traits are not modulated in panels A–C, resulting in regression lines that overlap in kinematic space. In contrast, component kinematic traits are modulated in panels D–F, as indicated by a shift in the trait space occupied by the alternative context (here, shown as a shift on both axes, to represent maximal separation). Regardless of whether component kinematic traits are modulated, integration may (B, C, E, F) or may not (A, D) also be modulated. If integration is modulated, it could be either in degree, represented by changes in slope (B, E), or in presence or absence, represented by slopes that are or are not different from zero, respectively (C, F). A and D show two alternatives, where integration is either not present (and therefore not modulated; case 1) or present but not modulated (case 2).

Higham, 2014). However, bluegill sunfish retain a small mouth, conducive to forceful suction (Holzman *et al.*, 2012), and suffer a reduction in accuracy and success when capturing live evasive prey (Kane & Higham, 2014). Given that modulation across non-evasive prey types might be attributable primarily to locomotor modulation (Moran *et al.*, 2018), we suggest that poor success with evasive prey might be the result of a limitation in the ability to integrate modulated performance traits, which reduces the ability to position the suction volume relative to this prey type (Kane & Higham, 2014). In this case, we expect that evasive and non-evasive prey types will elicit alternative locomotor and feeding kinematic outcomes and that integration will be weaker or absent with evasive prey (Fig. 1E, F).

MATERIAL AND METHODS

Prey capture trials

All experimental procedures were approved by the Institutional Animal Care and Use Committee at Clemson University, where all filming occurred. Sub-adult bluegill sunfish (*L. macrochirus*; four individuals, 9.13 ± 0.73 cm standard length, 22.7 ± 4.47 g) were

seined from Issaqueena Lake (Clemson University Experimental Forest, Clemson, SC, USA). We note that seven individuals were collected but we were not able to obtain complete datasets for three individuals, and individual identities provided throughout are not sequential. Fish were housed individually in the laboratory in 38 L aquaria maintained at 24 °C for ≥ 2 weeks before filming. Fish were fed a diet of commercially available frozen food supplemented with live juvenile wild-type sailfin mollies (*Poecilia latipinna*) every 1–3 days as available.

To record prey capture behaviour, bluegill sunfish were transferred to a 75 L filming tank and allowed to acclimate for a minimum of 24 h. The filming tank contained a divider to limit the filming arena to 53 cm × 32 cm × 29 cm and was mounted on a stand with a mirror placed at an angle of 45° underneath the tank to capture both lateral and ventral views with two synchronized cameras at 500 frames/s (1080 × 1080 pixels, Photron APX-RS; Photron USA Inc., San Diego, CA, USA). Depending on differences in the willingness of fish to feed and our ability to obtain usable recordings from each individual, feeding trials occurred over 2–7 days of filming. Fish were allowed a maximum of five or six successful prey captures per day, avoiding visible distension of the abdomen and the potential for effects of satiation (Essington *et al.*, 2000; Sass & Motta, 2002). The bluegill sunfish were offered non-evasive, free-floating, cut pieces of thawed frozen shrimp or evasive, live, untethered, wild-type juvenile mollies. Shrimp pieces were dropped into the tank by hand, whereas mollies were poured in from a small dish while the bluegill sunfish were held at the opposite end of the tank (a hand was held above the tank as if it contained food). In addition to encouraging the fish to use potentially extreme capture kinematics, these prey types were chosen to induce feeding in the water column, with minimal obstruction to the suction flow field. Prey types were presented alternately but were not randomized formally. Prey size for each individual ranged from 0.03 to 0.17 g for non-evasive prey and from 0.02 to 0.09 g for evasive prey and easily passed through the open gape without obstruction.

A total of 14–36 feeding attempts per fish were recorded. A subset of trials were chosen for analysis that met the following criteria: both videos were in focus and the structural features used to determine kinematics were visible throughout; the bluegill sunfish was stopped before its approach towards the prey (facilitating determination of the start of capture); prey were visible throughout the duration of the trial until capture, and the prey capture event occurred away from the sides or bottom of the tank. This resulted in five or six trials per individual per prey type being selected for analysis, for a total of 41 analysed trials. All non-evasive prey trials resulted in successful captures; for evasive prey trials, a total of eight unsuccessful and 13 successful trials were analysed, including two missed attempts per individual.

QUANTIFICATION OF KINEMATICS

To determine locomotor and feeding kinematics, trials were digitized (Fig. 2) using DLTdv5 (Hedrick, 2008) in Matlab (R2012a; The MathWorks, Inc., Natick, MA, USA). The start of the sequence began at the first sign of forward movement by the predator (excluding orientation before forward acceleration) and ended at maximum pectoral fin abduction during braking after the feeding event. The position of points that were not directly visible in ventral view (P01, P06, P07 and P08) was estimated based on anatomical landmarks and the three-dimensionally calibrated predicted location. To minimize digitizing error, the digitized tracks were overlain in DLTdv5 and inspected visually for smoothness and accuracy, to the nearest pixel. Once imported into Matlab, raw points (in pixels) were calibrated (in centimetres) and smoothed using a quintic spline in the curve-fitting toolbox. Tolerance values were adjusted manually (minimum, 0.001; maximum, 0.02; mean ± SD, 0.022 ± 0.031), and the pre- and post-smoothing data were visually inspected for similarity before acceptance of the smoothed values. Subsequent kinematic measurements and calculations were also performed in Matlab.

The feeding (FEED) dataset consisted of measurements describing movements of individual cranial components, such as the jaws, neurocranium, hyoid and operculum (Fig. 2), that together generate the suction outcome (Day *et al.*, 2015). Measurement of movement in these components represents a proxy for suction performance, because suction cannot be observed directly in the absence of complex experimental equipment (Ferry-Graham *et al.*, 2003; Day *et al.*, 2005, 2007; Higham *et al.*, 2006a, b). Kinematic traces were determined for gape (in centimetres; distance between P01 and P02), upper jaw protrusion (in centimetres; distance between P06 and P01), hyoid displacement (in centimetres; distance between P06 and P04), opercular expansion (in centimetres; perpendicular distance between P05 and the midline, drawn from P09 to the midpoint of the line describing gape) and cranial rotation (in degrees; angle formed by P06, P07 and P08). Measurements were taken from these traces to reflect the performance of buccal expansion and suction behaviours: peak gape distance; time to peak gape (duration from mouth opening to peak gape); peak mouth aperture area and area at the time of peak gape (in square centimetres; area of the ellipse formed using gape and the perpendicular distance from P03 to gape); peak upper jaw protrusion and protrusion at

the time of peak gape (the upper jaw often protracted, then retracted slightly near peak gape); peak hyoid displacement; peak cranial rotation and rotation at the time of peak gape (minimum internal angle); and peak opercular expansion. Additionally, the time to all peaks (in milliseconds; standardized relative to the time of peak gape) was also recorded. Timing variables (in milliseconds) were standardized by subtracting them from the time of peak gape, resulting in negative values occurring before peak gape and positive values occurring afterwards, with peak gape occurring at time 0 ms.

The locomotor (LOCO) dataset consisted of measurements describing predator whole-body movement at the estimated location of the centre of mass (Fig. 2, P09). The location of the centre of mass of bluegill sunfish has been demonstrated by others (Tytell & Lauder, 2008) and was not determined empirically here. The estimated location of this point was identified visually relative to landmarks such as fin locations. Predator velocity (in centimetres per second; change in displacement with time) and acceleration
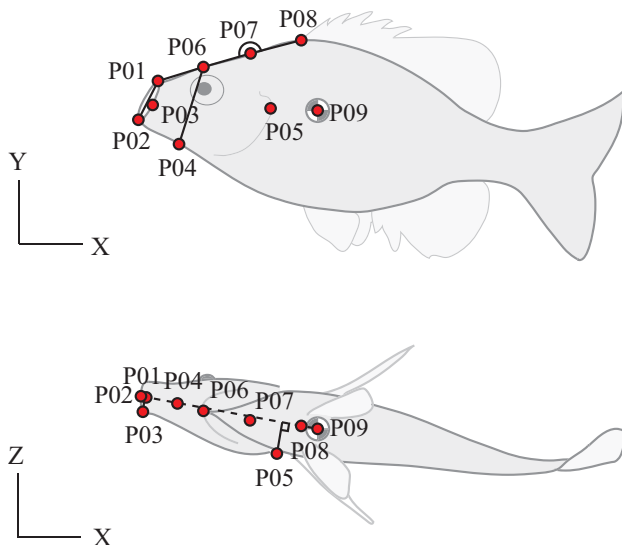

Figure 2. Points digitized from lateral (top panel) and ventral (bottom panel) camera views: P01, anterior border of the premaxilla (upper jaw); P02, anterior border of the dentary (lower jaw); P03, ventral border of the anteriorly protracted maxilla (lateral border of the mouth aperture); P04, anterior border of the hyoid apparatus; P05, posterior margin of the opercular flap; P06, a landmark placed directly above the eye on the neurocranium; P07, estimated inflection of the neurocranium, as identified along the dorsal profile of the skull; P08, anterior insertion of the dorsal fin; P09, estimated fish centre of mass. P09 was estimated visually using landmarks such as fin locations. Points were reconstructed in three dimensions to perform calculations for kinematic variables.

(in centimetres per second squared; change in velocity with time) were calculated from this single point. Measurements were taken from traces to reflect the performance of locomotor behaviours throughout the prey capture event: mean approach velocity (before the time of mouth opening); magnitude of velocity and acceleration at the time of peak gape; peak velocity (across the entire sequence); peak acceleration (across the entire sequence); peak deceleration (across the entire sequence); and time of each of these peak events.

MODULATION OF KINEMATICS

Confirmation of the modulation of kinematics across prey types was determined using a multivariate analysis of variance (MANOVA) and post-hoc ANOVAs. Before performing the analyses, the individual variables in both FEED and LOCO datasets were standardized to unit variance to facilitate comparison across variables of different magnitudes and measurement types. For each MANOVA (one for feeding and one for locomotor variables), the response included the standardized variables in the FEED or LOCO datasets and individual identity, prey type and the interaction were included as predictors. MANOVAs were performed using the 'fit model' platform with the 'MANOVA' personality and 'identity' response in JMP (v.13.1.0; SAS Institute, Inc., Cary, NC, USA). Differences in kinematics between prey types were detected as a significant prey type effect ($P < 0.05$) in multivariate and post-hoc univariate models. A principal components analysis (PCA) was used to summarize and visualize these kinematic differences. After correcting for a magnification effect, performance traits varied more than body size, and most variables showed no significant relationship with size (Supporting Information, Appendix S1; Fig. S1). Additionally, given that body size was similar across individuals, size was not included as an explanatory factor.

MODULATION OF INTEGRATION

To account for the potential for multiple feeding and locomotor traits to be integrated, integration was determined by assessing the statistical association between multivariate feeding and locomotor datasets using partial least squares (PLS) ordination (following the recommendation by Kane & Higham, 2015). In this analysis, predictor and response matrices are used as input, and each resulting singular axis (SA) is composed of pairs of scores that relate to either predictor or response matrices. To determine integration, SA1 response and SA1 predictor axes can then be used to visualize and test the relationship between matrices (Kane & Higham, 2015). Given

that regressions provide additional information about the relationship between traits (namely slope), allowing additional statistical insights compared with correlations (Montuelle & Kane, 2019), we rely on regression, rather than correlation, analyses after PLS ordination to demonstrate integration and the differences between prey types.

To preserve variation across trials and allow subsequent testing of this variation in the general linear model (GLM) regressions, PLS ordinations were performed on centred and scaled variables without accounting for individual or prey type. We note that we did examine the consequences of performing these analyses using alternative approaches to the PLS analysis, but these did not change our interpretations and we have chosen to rely on this more simple model throughout. Here, we relied on locomotor kinematics as the predictor and feeding kinematics as the response, but we also performed the analysis in reverse to confirm that the directionality chosen was represented by our data (Supporting Information, Appendix S2 and Tables S1-S5). The number of significant singular axes for each PLS was determined using the 'leave-one-out' method of cross-validation (Wold *et al.*, 2001; Krishnan *et al.*, 2011). To quantify integration between the locomotion and feeding datasets, we used general linear regression models with the (predictor singular axis + prey + individual + all interactions) as predictors of the response singular axis and reduced the model by removing non-significant interaction effects. Partial eta-squared (η^2) statistics were calculated for each predictor to determine the effect size relative to other predictors (Maher *et al.*, 2013). The variables driving integration were determined by examination of the loadings on the corresponding SA. All statistical tests were performed in JMP (v.13.1.0).

RESULTS

BLUEGILL SUNFISH MODULATE PREY CAPTURE KINEMATICS

Bluegill sunfish captured evasive and non-evasive prey types using modulated kinematics, as expected (Tables 1 and 2; Fig. 3). The duration of the entire prey capture event was 68.9% shorter when capturing evasive prey (non-evasive, 927.2 ± 258.4 ms; evasive, 639.2 ± 198.7 ms) and had a proportionally shorter approach and longer strike (mouth opening to peak gape) during capture of evasive prey (approach: non-evasive, 80.1 ± 4.7% vs. evasive, 66.4 ± 8.6%; strike: non-evasive, 19.9 ± 4.7% vs. evasive, 33.6 ± 8.6%). MANOVA models were significant predictors of both feeding (whole model: Wilks' λ = 0.0009, $F_{105,130.92}$ = 2.46,

$P < 0.0001$) and locomotor kinematics (whole model: Wilks' λ = 0.0301, $F_{63,146.91}$ = 2.01, $P = 0.0003$). Feeding kinematics differed among individuals (individual effect: Wilks' λ = 0.014, $F_{45,57.225}$ = 4.09, $P < 0.0001$) and prey types (prey type effect: $F_{15,19}$ = 5.25, $P = 0.0005$), and these differences were also reflected in the PCA (Fig. 3A). Differences among individuals were not detected among locomotor kinematics (individual effect: Wilks' λ = 0.261, $F_{27,73.655}$ = 1.59, $P = 0.0605$), where movements diverged primarily between prey types (prey type effect: $F_{9,25}$ = 11.21, $P < 0.0001$). Similar divergence was again reflected in the PCA (Fig. 3B). Interactions between individual and prey type were not significant for either dataset (Table 2).

Evasive prey elicited greater kinematic magnitudes in both feeding and locomotion, and differences among individuals reflected differences in the tendency to use this evasive prey strategy (Tables 1 and 2). When capturing evasive prey, post-hoc ANOVAs indicated that the magnitude of cranial expansion was greater (gape size, jaw protrusion, hyoid depression and opercular expansion) and achieved more quickly, body velocity and acceleration were greater, the timing of peak velocity and acceleration was closer to the time of peak gape, and deceleration was reduced (Table 2; Fig. 4). Differences among individuals were observed in the same feeding kinematic variables, with the exception of differences among individuals in jaw protrusion and cranial rotation instead of hyoid depression (Table 2; Fig. 4). The feeding PCA results showed similar divergence in kinematics, but the time of peak jaw protrusion, peak hyoid depression and peak opercular expansion were not recovered on principal component (PC)1 (Table 2). These variables were recovered on PC2, alongside additional jaw protrusion and cranial rotation feeding kinematic traits that were not significant in post-hoc ANOVA tests (Table 2). For locomotor kinematics, evasive prey elicited faster velocities, acceleration and deceleration, which occurred closer to the time of peak gape (Table 2; Fig. 5). The locomotion PCA results recovered similar differences in kinematics on PC1 (Table 2).

Variables describing the timing of cranial expansion that occurs at or after jaw opening generally did not differ among prey types or individuals, suggesting a constraint on the temporal dynamics of the posterior wave of expansion through the mouth during the generation of suction. Therefore, changes in the magnitude and rate of expansion primarily drive differences in feeding kinematics across prey types. In contrast, both timing and magnitude of swimming kinematics were modulated across prey types. These results suggest that the primary differences in kinematics across prey types in bluegill sunfish are in the degree and rate of mouth expansion, the speed with which bluegill sunfish approach their prey and

Table 1. Means and standard errors for kinematic traits

	Non-evasive		Evasive	
	Mean	SE	Mean	SE
Peak gape (cm)	0.85	0.05	1.00	0.04
Time to PG (ms)	47.7	3.1	29.1	1.5
Gape aperture area at PG (cm^2)	16.26	1.99	21.63	1.20
Peak gape aperture area (cm^2)	16.26	1.99	21.64	1.20
Time of peak gape aperture area (ms relative to PG)	−0.1	0.2	0.4	0.2
Jaw protrusion at PG (cm)	0.198	0.020	0.188	0.018
Peak jaw protrusion (cm)	0.237	0.021	0.265	0.019
Time of peak jaw protrusion (ms relative to PG)	5	3.7	10.4	3.3
Peak hyoid depression (cm)	0.309	0.018	0.400	0.014
Time of peak hyoid depression (ms relative to PG)	4.2	1.5	2	0.5
Cranial rotation at PG (°)	9.57	0.81	10.01	0.71
Peak cranial rotation (°)	10.21	0.79	10.86	0.62
Time of peak cranial rotation (ms relative to PG)	−1.4	1.8	0.2	1.6
Peak opercular expansion (cm)	0.47	0.04	0.69	0.06
Time of peak opercular expansion (ms relative to PG)	31.6	1.5	33.2	1.6
Velocity at PG (cm/s)	20.8	2.8	56.5	3.7
Acceleration at PG (cm/s^2)	−331.5	37.3	−123.3	143.3
Mean approach velocity before mouth opening (cm/s)	27.7	2.1	35.9	2.2
Peak velocity (cm/s)	37.8	2.8	62.1	3.5
Time of peak velocity (ms relative to PG)	−310.7	28.0	−55.2	16.7
Peak acceleration (cm/s^2)	397.1	76.4	1032.5	122.7
Time of peak acceleration (ms relative to PG)	−534.6	32.0	−161.1	40.3
Peak deceleration (cm/s^2)	−521.6	89.9	−1224.1	121.3
Time of peak deceleration (ms relative to PG)	23.5	8.1	24.5	4.4

Abbreviations: PG, peak gape.

the timing when this speed occurs relative to mouth opening, and the degree to which bluegill sunfish decelerate during prey capture. Individuals are less likely to differ in the timing of feeding kinematics or locomotor kinematics, suggesting that variability among individuals exists primarily in the use of mouth expansion to generate suction, reflecting differences in the propensity to use relative evasive or non-evasive prey capture strategies.

INTEGRATION DIFFERS AMONG INDIVIDUALS MORE THAN ACROSS PREY TYPES

A partial least squares model using locomotor kinematics as a predictor and feeding kinematics as a response was preferred and used throughout (see Supporting Information, Appendix 2 and Table S1). Only one singular axis was recovered and showed that locomotor kinematics explained 56.53% of the covariation, whereas feeding kinematics explained 14.19%. Variables loading strongly on each axis mirrored those where differences were supported between individuals and/or prey types (Table 2). Specifically, positive loadings for each dataset

indicated an increase in mouth expansion, velocity and acceleration, and timing of acceleration near that of peak gape, whereas negative values indicated greater time to peak gape, later hyoid depression (which did not differ between individuals or prey types in prior analyses) and increased deceleration (Table 2).

Integration of kinematics showed differences attributable to both individuals and prey types. The reduced full factorial version of the PLS (model 1, run 6) explained 26.6% more of the variation in locomotion scores than the no factor version (model 1, run 1), which had the lowest proportion of variance explained (Supporting Information, Table S2). The reduced model also had the lowest Akaike information score corrected for small sample size, indicating that it provided the best explanation of the versions tested. An integrated relationship was supported, but additional variation was attributed to differences among individuals and interactions between predictors and prey type or individual identity (Fig. 6; Table 3). An interaction between predictors and prey type suggests that prey types induced differences in integration (partial η^2 = 0.030; Fig. 6B), but the interaction with individual (partial η^2 = 0.067; Fig. 6C) had more

Table 2. Statistical results for MANOVA, post-hoc ANOVA, PCA and PLS analyses

	MANOVA and post-hoc ANOVAs					PCA		PLS
	Whole model	Intercept	Individual	Prey type	Individual * prey type	PC1	PC2	SA1
Feeding								
Percentage of variation explained (PCA and PLS)	—	—	—	—	—	26.91	21.77	14.19
Feeding kinematic variables (MANOVA)	**< 0.0001**	1	**< 0.0001**	**0.0005**	0.2047	—	—	—
Peak gape	**< 0.0001**	0.6681	**< 0.0001**	**< 0.0001**	0.2645	**0.425**	−0.162	**0.388**
Time to PG	**< 0.0001**	0.8568	**0.0026**	**< 0.0001**	**0.0209**	**−0.302**	0.002	**−0.540**
Gape aperture area at PG	**< 0.0001**	0.8542	**< 0.0001**	**0.0021**	**0.0013**	**0.404**	−0.176	**0.294**
Peak gape aperture area	**< 0.0001**	0.8544	**< 0.0001**	**0.0021**	**0.0013**	**0.405**	−0.176	**0.294**
Time of peak gape aperture area	0.2618	0.974	0.3873	0.0991	0.3308	0.256	−0.060	0.182
Jaw protrusion at PG	0.6732	0.9557	0.239	0.743	0.9506	−0.019	**0.397**	−0.120
Peak jaw protrusion	0.3083	0.947	0.0856	0.2739	0.9519	0.119	**0.484**	0.059
Time of peak jaw protrusion	**0.0027**	0.8945	**0.0003**	0.1424	0.737	0.046	**0.381**	0.110
Peak hyoid depression (cm)	**0.0212**	0.963	0.3008	**0.0004**	0.8803	0.214	0.156	**0.328**
Time of peak hyoid depression	0.1706	0.9543	0.1657	0.1599	0.3208	−0.191	0.145	**−0.231**
Cranial rotation at PG	0.1094	0.9933	0.027	0.647	0.5064	0.293	**0.304**	0.172
Peak cranial rotation	**0.0481**	0.9655	**0.0105**	0.4934	0.4727	**0.323**	0.297	**0.187**
Time of peak cranial rotation	0.1631	0.9232	0.0813	0.4212	0.3631	0.078	0.246	0.104
Peak opercular expansion	**0.0014**	0.8681	**0.0073**	**0.0013**	0.3008	0.194	**−0.280**	**0.293**
Time of peak opercular expansion	0.1035	0.9827	0.2196	0.4318	0.0648	−0.049	−0.074	0.014
Locomotion								
Percentage of variation explained (PCA and PLS)	—	—	—	—	—	56.56	14.9	56.53
Locomotor kinematic variables (MANOVA)	**0.0003**	1	—	**< 0.0001**	0.3174	—	—	—
Velocity at PG	**< 0.0001**	0.7753	0.0605	**< 0.0001**	0.1566	**0.421**	−0.149	**0.424**
Acceleration at PG	**0.019**	0.9151	**0.0467**	**< 0.0001**	0.0723	0.131	**0.661**	0.122
Mean approach velocity before mouth opening	0.0878	0.9181	**0.0378**	0.0967	0.5681	0.289	**−0.499**	0.293
Peak velocity	**< 0.0001**	0.8137	0.2396	**0.0114**	0.2581	**0.405**	−0.279	**0.408**
Time of peak velocity	**< 0.0001**	0.8064	0.0789	**< 0.0001**	0.121	**0.37**	0.168	**0.370**
Peak acceleration	**0.0055**	0.8955	0.1694	**0.0001**	0.4477	**0.371**	0.133	**0.367**
Time of peak acceleration	**< 0.0001**	0.8684	0.3422	**< 0.0001**	0.6188	**0.347**	**0.334**	**0.347**
Peak deceleration	**0.0002**	0.8291	0.4154	**< 0.0001**	0.6744	**−0.403**	−0.032	**−0.400**
Time of peak deceleration	0.3615	0.9984	**0.0126**	**< 0.0001**	0.2944	−0.030	0.234	−0.029

Values for MANOVA and post-hoc ANOVAs are P-values from statistical tests. Significance was determined at $P < 0.05$ and is highlighted in bold. Values for PCA and PLS tests are loading scores, with strong loadings highlighted in bold.
Abbreviations: MANOVA multivariate analysis of variance; PC, principal component; PCA, principal components analysis; PG, peak gape; PLS, partial least squares; SA, singular axis.
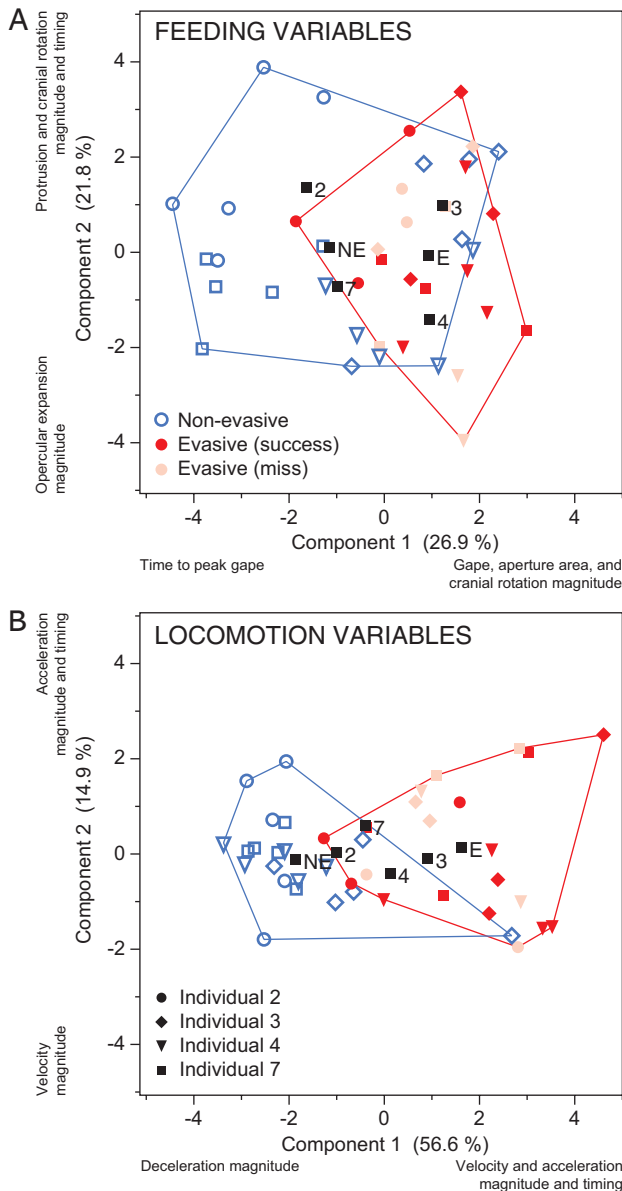
Figure 3. Modulation of feeding (A) and locomotor (B) kinematic variables as demonstrated using principal components analysis. Symbol shapes indicate different individuals. Open blue shapes, non-evasive prey; dark filled red shapes, evasive prey successful captures; light filled red shapes, evasive prey unsuccessful captures. The space encompassed by trials with each prey type is outlined with corresponding colours. Average scores for individuals and prey types (E, evasive; NE, non-evasive) are shown with black filled squares. Loadings for each variable are given in Table 2. Component 1 separates trials by prey type for each dataset. For feeding variables, component 2 separates individuals.

than double the effect size on integration (Table 3). Additionally, the greatest effect size was attributed to individual identity, at slightly > 13% of the total sum

of squares of the GLM (Table 3). Therefore, differences in kinematics among individuals affect not only the magnitude of mouth expansion, but also the integration with locomotor kinematics. Based on differences in slopes from simple linear regressions, individuals 2 and 7 are likely to be more integrated than individuals 4 and 3, suggesting that the magnitude of modulation in feeding as a result of locomotion is more substantial (Fig. 6C). Exclusion of the individual × prey type interaction from the reduced GLM model (Supporting Information, Table S2) suggests that individuals show consistent integration across prey types and that the effects of prey type on integration are observed across individuals rather than within individuals. Therefore, modulation of kinematics in response to prey type does not result in modulation of integration, and differences in integration are driven by among-individual differences in integrated patterns.

DISCUSSION

INTEGRATION IS INFLEXIBLE WITHIN INDIVIDUALS, DESPITE MODULATED KINEMATICS

Our study confirms that bluegill sunfish modulate locomotor and feeding movements when capturing evasive and non-evasive prey types (Fig. 1D–F), as expected, but also shows that integration of these traits is present and conserved across capture of alternative prey types (Fig. 1D, scenario 2 if lines represent alternative prey types within an individual). In other words, kinematic traits are flexible, but integration between these traits is inflexible, and modulation of kinematics does not disrupt integration in bluegill sunfish.

An increase in kinematic effort is a useful strategy for capturing evasive prey (Norton, 1991, 1995; Holzman *et al.*, 2012). However, this ability may be constrained in bluegill sunfish, thereby increasing the functional demand for integration of locomotion with feeding and resulting in consistency across prey types. Capture of free-floating, non-evasive prey entails smaller, slower mouth opening coupled with a slower approach speed. This prey type might require only minimal force generation, allowing reduced kinematic effort and energy conservation (Vinyard, 1982). Alternatively, an increase in mouth size and reduction in mouth opening duration may require more effort (Camp & Brainerd, 2014; Van Wassenbergh *et al.*, 2015; Camp *et al.*, 2018) but increases the magnitude of suction force at the mouth aperture (Day *et al.*, 2005; Wainwright & Day, 2007; Holzman *et al.*, 2008a). Coupled with an increase in approach speed, the volume and reach of suction increase (Higham *et al.*, 2005, 2006a; Holzman *et al.*, 2008b, 2012), the probability of positioning the prey close to the mouth aperture (and strongest forces)
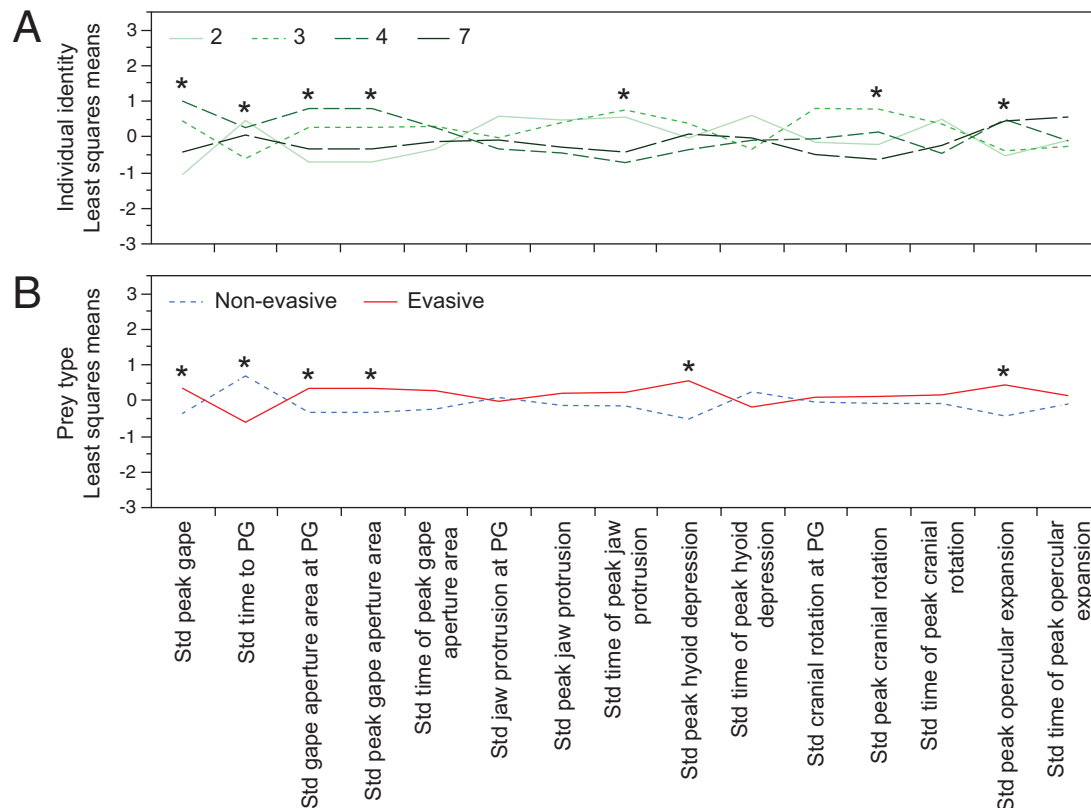
Figure 4. Least squares means of standardized feeding variables for individual identity (A) and prey type (B) main effects. Abbreviations: PG, peak gape; Std, standardized. *Significant ($P < 0.05$) univariate effects.

increases (Holzman *et al.*, 2008a), and the amount of time that prey has available to respond to a predator decreases, facilitating capture of evasive prey. However, bluegill sunfish retain suction-specialized traits, such as a small mouth aperture, that limit the total amount of modulation possible in the feeding system and increase the importance of mouth displacement speed (jaw and/or whole-body movement towards prey) for aligning suction force with prey position (Holzman *et al.*, 2008b; Holzman & Wainwright, 2009). Therefore, integration of locomotion with feeding behaviours might be especially pervasive and necessary in bluegill sunfish or other suction specialists.

The feeding kinematics reported here for juvenile bluegill sunfish are typical for this species and for other suction-feeding fishes and can be considered representative. The feeding kinematics are similar to, or less than, kinematics reported for adult bluegill sunfish, including comparisons across polymorphic and hybrid populations (Gillis & Lauder, 1995; McGee *et al.*, 2015; Moran *et al.*, 2018), but fit within the ontogenetic predictions for bluegill sunfish at this body size (Holzman *et al.*, 2008a). To capture untethered, live, evasive prey, our bluegill sunfish used a larger gape that opened faster, coupled with a faster approach speed. These changes with evasive prey are similar to those observed when similar-sized juvenile bluegill sunfish captured prey with competitors present (Pfeiffenberger & Motta, 2012) and are congruent with the direction of modulation observed in cheek-lined wrasse (*Oxycheilinus diagrammus*), kelp greenling (*Hexagrammos decagrammus*), blue-green damselfish (*Chromis viridis*) and Sacramento perch (*Archoplites interruptus*) (Nemeth, 1997a, b; Vinyard, 1982; Coughlin & Strickler, 1990; Ferry-Graham *et al.*, 2001), and in asp (*Aspius aspius*), which modulate kinematics when evasive prey perform an escape response (Van Wassenbergh & De Rechter, 2011). Our sample of four fish is small, but the consistency of kinematic traits with these previous studies suggests that our data might be representative more broadly. Additionally, given that kinematic modulation along a single integrated relationship was present in all individuals and that these fish varied in magnitudes of this relationship to encompass the range of possible variation in this trait (negligible to strong), the addition of individuals would probably not have altered our conclusions. Bluegill sunfish are often used as a model of fish swimming and feeding biomechanics, within which mechanisms can be understood and hypotheses
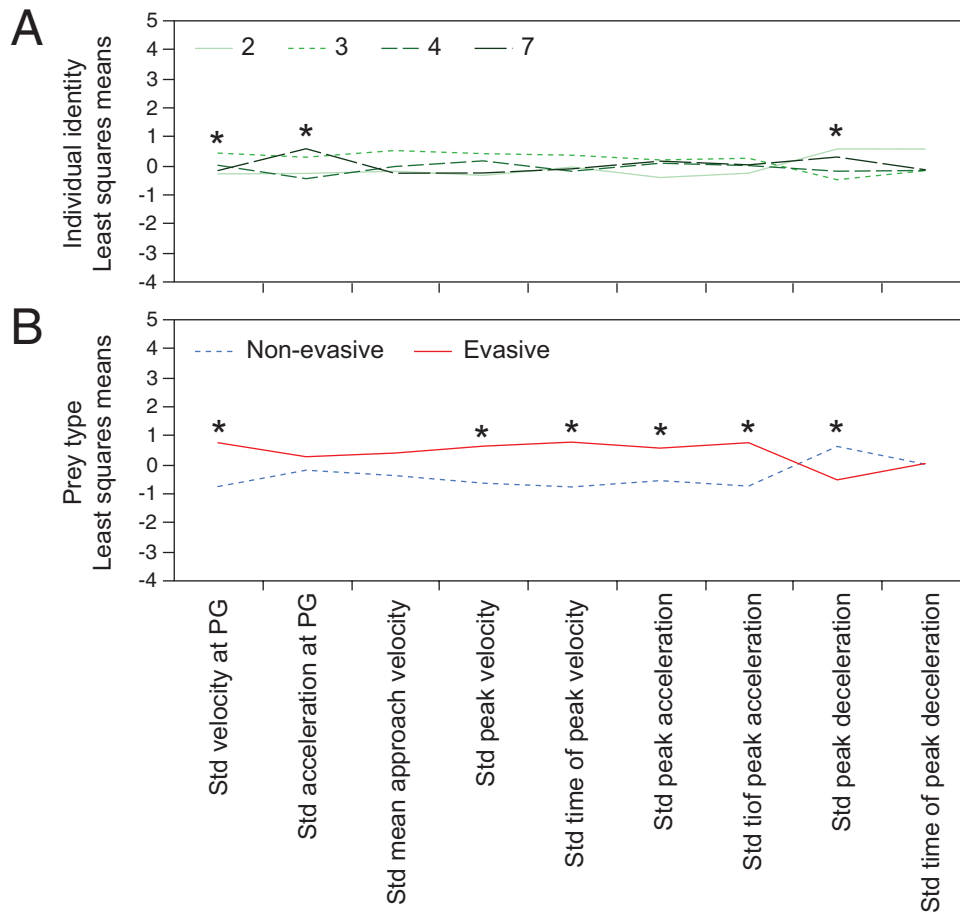
Figure 5. Least squares means of standardized locomotion variables for individual identity (A) and prey type (B) main effects. Abbreviations: PG, peak gape; Std, standardized. *Significant ($P < 0.05$) univariate effects.

can be developed and applied more broadly. For this reason, we suggest that our results with bluegill sunfish demonstrate that kinematic integration, and its variation among individuals, might be prevalent among fishes and deserves attention in future studies.

It is generally understood and broadly supported that the inclusion of locomotor behaviours is important for understanding feeding behaviours and diversification in fishes (Weihs, 1980; Muller & Osse, 1984; Van Leeuwen, 1984; Norton, 1991; Wainwright *et al.*, 2001; Higham *et al.*, 2005; Ferry *et al.*, 2015; Longo *et al.*, 2015) and in other vertebrates (Webb, 1984; McElroy *et al.*, 2008; McBrayer & Wylie, 2009; Falk *et al.*, 2014; Goldbogen *et al.*, 2015; Montuelle & Kane, 2019). Swimming speed and mouth size can act as key drivers of prey capture strategies in suction-feeding fishes (Higham, 2007a, b; Higham *et al.*, 2007; Kane & Higham, 2011; Oufiero *et al.*, 2012; Kane *et al.*, 2019a, b), and our study provides further support for this idea, finding a correlation between locomotor and feeding kinematics during prey capture in bluegill sunfish, driven by swimming speed and mouth size

(Table 2). However, we extend this understanding by demonstrating that an integrated phenotype might be inflexible across contexts within individuals (Wainwright *et al.*, 2008). Given that modulation depends on the ability of an individual to detect and respond to prey (Aerts, 1990; Van Wassenbergh & De Rechter, 2011), rather than on population-level differentiation in capture strategies, we rely on the lack of differences within individuals to conclude that integration is maintained across prey types. The ability to modulate component kinematics while maintaining whole-organism function may be an example of functional redundancy, permitting bluegill sunfish to exploit alternative prey resources while accomplishing a complex behaviour. Therefore, the functional redundancy described in morphological traits used to accomplish suction (Holzman *et al.*, 2011) might extend to locomotor and feeding kinematic traits used to accomplish prey capture.

Suction is a specialized behaviour relative to other feeding modes (Mehta & Wainwright, 2007; Collar *et al.*, 2014), which might constrain the range of
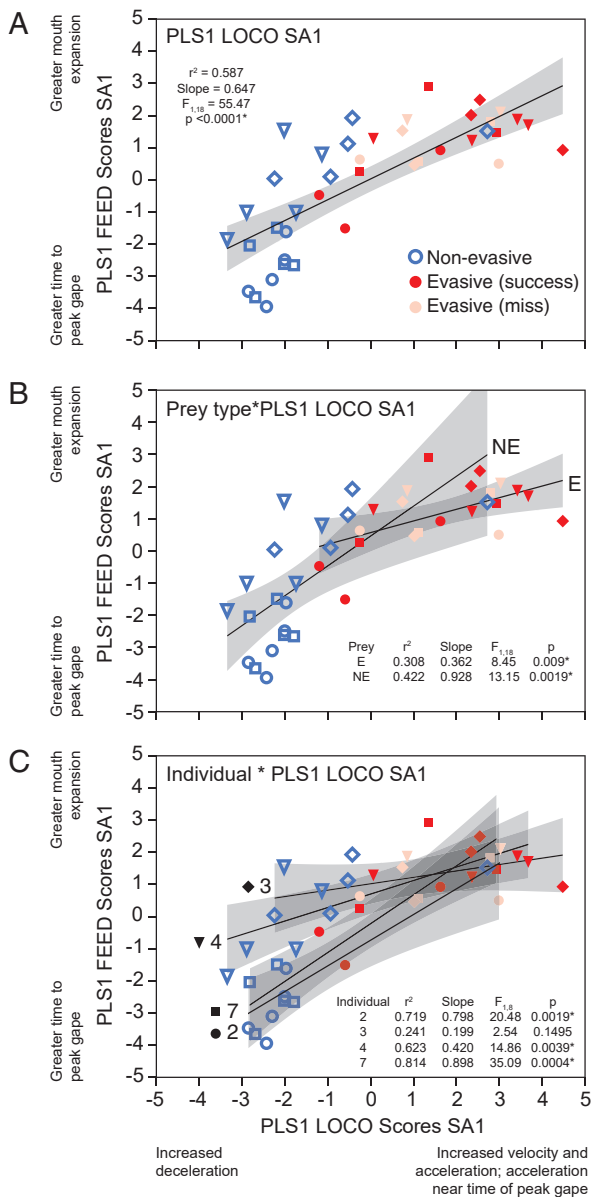
Figure 6. Multivariate integration using partial least squares ordination followed by regression analyses. Conclusions are based on general linear models (Table 3), but simple linear regressions and associated statistics are shown here for visualization purposes. Three significant model effects are shown using the same data with alternative relationships visualized, as follows: A, the ability for locomotor performance scores to predict feeding performance scores (integration, overall); B, the difference in integration as a result of the interaction with prey type (differences in integration at the population level); and C, the difference in integration as a result of the interaction with individual identity (differences in integration among individuals). Regressions are shown with confidence intervals for all trials, prey types or individuals (black lines). Symbol shapes indicate different individuals (indicated numerically); open blue symbols, non-evasive trials (NE); filled red symbols, evasive

available locomotor behaviours that can be used in combination (Webb, 1984; Kane & Higham, 2015) and mean that integration is required or beneficial in suction feeders, regardless of context. The repeated presence of integrated relationships in other suction-feeding vertebrates, including secondarily aquatic beluga whales (*Delphinapterus leucas*), supports this possibility (Higham *et al.*, 2007; Oufiero *et al.*, 2012; Kane & Higham, 2015; Longo *et al.*, 2015; Kane *et al.*, 2019a, b). However, the presence of an integrated and inflexible relationship in low-predation Trinidadian guppies (*Poecilia reticulata*) using biting and suction strategies for prey capture (Kane *et al.*, 2019a) suggests that the reliance on an integrated relationship might be applicable beyond suction behaviours. In fact, integration has been observed recently in a mudskipper (*Periopthalamus barbarus*) that uses biting to capture prey on a terrestrial substrate (Kane *et al.*, 2019a), a feeding mode that is common for terrestrial vertebrates and might also benefit from integration (Montuelle & Kane, 2019). However, these same studies range in the strength of the relationship observed between performance traits, suggesting that, in addition to the presence and consistency of integration, the degree of integration might provide an ecologically relevant source of variation.

INTEGRATION IS VARIABLE ACROSS INDIVIDUALS

Bluegill sunfish varied in the degree of modulation of kinematics, and this variation coincided with variation among individuals in the integrated relationship between kinematic traits (Table 3; Fig. 6C). The individual effect on integration in bluegill sunfish does not match any of the scenarios in Figure 1 exactly, but Figure 1C might be the best representation of the magnitude of variation in integration among individuals, despite this scenario depicting a lack of modulation in performance traits (which was, in fact, supported by our data).

Differences among individuals appear to be attributable, at least in part, to individuals preferring

prey trials (E); light filled symbols, unsuccessful evasive prey trials. In all three cases, kinematics are modulated with prey type, consistent with Figure 1D–F. However, modulation of integration, consistent with Figure 1E, occurs only at the population level; integration is not modulated with performance within individuals, consistent with Figure 1D. Given that modulation occurs as an individual response to variation in context, we rely on the individual-level result to conclude that integration is not modulated with prey type in these bluegill sunfish, but does vary in degree among individuals. Abbreviations: FEED, feeding kinematics; LOCO, locomotor kinematics; PLS, partial least squares; SA, singular axis.

Table 3. General linear model effect statistics for differentiation in integration

Effect	d.f.	Sum of squares	F	P-value	η^2	Partial η^2
PLS1 LOCO SA1	1	12.4067	18.0865	**0.0002**	0.086	0.079
Individual	3	18.83573	9.1529	**0.0002**	0.130	0.115
prey	1	1.368093	1.9944	0.1678	0.009	0.009
Individual*PLS1 LOCO SA1	3	9.717608	4.7221	**0.0079**	0.067	0.063
prey*PLS1 LOCO SA1	1	4.388683	6.3978	**0.0167**	0.030	0.029

Significance was determined at $P < 0.05$ and is highlighted in bold.
Abbreviations: d.f., degrees of freedom; LOCO, locomotor kinematics; η, Eta statistic; PLS, partial least squares; SA, singular axis.

to use different amounts of mouth expansion for non-evasive prey (spanning the feeding PLS axis) but converging on maximum mouth expansion for evasive prey (positive PLS scores only). Therefore, variation in regression slopes is dependent primarily on variation in modulation of feeding kinematic outcomes (Fig. 6C). For example, individuals 2 and 7 display greater modulation of feeding kinematics across prey types, and these individuals display steeper integrated regression slopes. Alternatively, the lack of integration found in individual 3 coincides with a reliance on feeding kinematics that occur at a morphological maximum, where increases in approach velocity cannot be matched with increased mouth expansion. In this way, the effect of prey types on bluegill sunfish kinematic integration is apparent in the differences in how individuals achieve integration across prey types, rather than in the modulation of integration in response to prey types. Given that prey capture is an ecologically relevant behaviour, integration (and its variation) might also be relevant ecologically and evolutionarily in fishes.

Variation in traits among individuals during an ecologically relevant behaviour, such as prey capture, can have implications for mediating ecological interactions and may provide a source of variation upon which selection can act within populations. For example, variance in the specialization of individuals relative to the population mean can be important for mediating intraspecific competition or the response to selection (Bolnick *et al.*, 2003; Svanbäck & Bolnick, 2005, 2007; Laskowski & Bell, 2013). Mediating these interactions is likely to be common and important in bluegill sunfish, because within-population polymorphism and specialization in diet, foraging behaviour and locomotor behaviour have been demonstrated repeatedly (Werner *et al.*, 1981; Ehlinger & Wilson, 1988; Ehlinger, 1990; Wilson *et al.*, 1996; Fry *et al.*, 1999; Ellerby & Gerry, 2011; Gerry *et al.*, 2013; Hitchcock *et al.*, 2015). We extend these ideas to suggest that variation among individuals is also apparent in bluegill sunfish for emergent, whole-organism traits, such as kinematic integration.

Additionally, these differences may provide a source of variation that can be acted upon by selection and contribute to adaptive differences between populations or species (Kane *et al.*, 2019a, b).

The assumption in many kinematic studies is that variation among individuals is negligible or a nuisance variable in comparison to the main effects of interest in populations and, although it is accounted for, it is not often reported or discussed. The use of labour-intensive techniques, such as morphological reconstruction, surgical procedures or kinematic analysis, requires researchers to balance the time constraints of managing animals and analysing experimental outputs with the scale of their inferences. If the variation among group comparisons is expected to be greater than the variation among individuals within groups, emphasis is often given to maximizing the number of groups rather than the number of individuals. However, when examined, inter-individual variation can be significant and provide important biological information (Collins & Higham, 2017). Faced with constraints on the number of individuals that could be used, we chose to describe variation in kinematics using multiple trials per fish rather than a single trial from a larger number of individuals. In our best effort to reduce variation among individuals, we seined juvenile (assumed to be relatively naïve) fish from the same location in the same lake within a short time span. As a result, we expected group differences (prey types) to be greater than individual differences. However, we might have selected inadvertently for individual variation, because among-individual variation in diet may be highest in small bluegill sunfish collected along the margin of a lake owing to increased competition in this habitat (Fry *et al.*, 1999). Increased competition during prey capture attempts can result in higher-effort kinematics (larger, faster mouth opening and faster approach speed) in bold, competitively dominant fish (Pfeiffenberger & Motta, 2012), but it is unclear whether bold fish varied in the degree of modulation or how bold fish might differ in kinematics from shy fish. Our study suggests that examination of the variation across individuals, which may differ in personality

type or other traits, might be an important and often-overlooked source of variation in kinematics and prey capture that should be explored further.

INTEGRATION AS AN EMERGENT REGULATOR OF KINEMATIC OUTCOMES

Modulatory multiplicity of prey capture kinematics (Liem, 1978, 1979), or the behavioural ability to select kinematic outputs to match alternative demands, is common in animals (Anderson, 1993; Deban, 1997; Wilga & Motta, 1998; Ferry-Graham *et al.*, 2001; Flammang & Lauder, 2009; Domenici, 2010; Stayton, 2011; Van Wassenbergh & De Rechter, 2011; Gardiner & Motta, 2012; Montuelle *et al.*, 2012a; Seamone *et al.*, 2014) and is likely to be a reflection of both physiological and functional constraints. Changes in kinematic output are achieved through changes in muscle activation patterns (Lauder, 1980; Wainwright & Lauder, 1986; Sanderson, 1988; Matott *et al.*, 2005; Foster & Higham, 2014; Foster *et al.*, 2018) in response to sensory detection of environmental cues at long and short ranges (Aerts, 1990; Van Wassenbergh & De Rechter, 2011). Use of sensorimotor feedback in this way represents a 'bottom-up', physiological mechanism dictating realized performance, where variation among individuals can be attributable to variation in the ability to perceive the environmental context and coordinate a motor response (Birn-Jeffery & Higham, 2016; Collins & Higham, 2017). In this case, achieving an integrated functional response across systems is likely to be dependent on active neural coordination of motor outputs (Olsen *et al.*, 2019), and integration might be expected to vary based on variation in kinematic responses across contexts; essentially, kinematic outcomes regulate integration.

However, the alternative, that integration regulates kinematic outcomes, is also possible. Integration across traits may act as a functional constraint within which sensorimotor coordination of each functional system occurs, and higher-order integration can regulate kinematic outputs chosen to facilitate function. In other words, physiological mechanisms may permit modulation, but functional constraints unique to each individual (the slope of the integrated relationship) can dictate how modulation manifests. In this way, integration can represent a whole-organism functional output that may act as an emergent, 'top-down' regulator of realized kinematic output in each behavioural context (Korn, 2005). We note that this description of a functional constraint is more specific than the broad idea that systems must work together to achieve a common goal, because it describes how this general constraint is exhibited within an individual. Viewing integration as an emergent and variable organismal trait imposing constraints on component traits provides new insight into why individuals vary in observed kinematics.

Our work supports the idea that fish detect and respond to alternative prey using physiological modulation of kinematic output, but also supports the idea that the way in which these alternative responses are expressed in individuals might be constrained by their function at a higher, integrated, whole-organism level (Korn, 2005). In bluegill sunfish in the present study, modulation of kinematic traits does not coincide with flexibility of their integration and is not likely to be a product of specific combinations of kinematic traits. Instead, integration may be a constant trait at the whole-organism level that imposes limitations on how locomotor and feeding kinematics occur during each behaviour. In bluegill sunfish, individuals with a stronger relationship between swimming and feeding (as identified with slope) modulate feeding kinematics to a greater degree than those with a weaker relationship, and the observed kinematics in each individual might be constrained to occur along the regression line that describes the integrated relationship. For example, if individuals can use a large gape to capture prey, as they do with evasive prey, presumably they could also use a smaller gape if necessary. But this modulation of gape occurs only in individuals where the integrated relationship allows it (i.e. not in individual 3). However, both physiological and functional constraints are likely to operate in tandem to generate an integrated response. Deviation in integration among individuals, as observed in bluegill sunfish, may represent variation in an ability to achieve or use sensorimotor coordination (how behaviour is generated), variation in emergent regulatory integration as expressed at the organismal level (why behaviour occurs a specific way), or some combination of these factors. Furthermore, the presence of variation among individuals in this whole-organism trait suggests that integration may be exposed to selection and act as an important source of variation in prey capture.

The idea that functional integration might be a relevant trait for evolutionary processes is supported by work demonstrating variation in the degree of integration at species- and population-level scales. For example, the locomotor structures integrated with feeding in lizards differ depending on the portion of the prey capture event within which it is used (Montuelle *et al.*, 2012b), species of dolphins differ in whether the integrated relationship is represented by a positive or negative slope (Kane *et al.*, 2019a), species of marine sculpins differ in the number of univariate correlations between performance systems and in the number of multivariate axes of integration

(Kane & Higham, 2011, 2015), and largemouth bass (*Micropterus salmoides*) (Higham, 2007a) may have univariate integration that is nearly twice as strong as that currently observed in bluegill sunfish (bass, $r^2 = 0.58$ vs. bluegill sunfish from the present study, $r^2 = 0.29$). In addition to divergence between species, integration in derived populations of guppies evolves repeatedly and convergently from a non-integrated ancestral population (Kane *et al.*, 2019a, b). These examples highlight patterns of divergence in integration at or above the population level, but divergence at these levels is reliant on variation among individuals within populations, upon which selection can act. Our study demonstrates support for this necessary level of variation. However, the generation and maintenance of phenotypic variation among individuals within a population can be attributable to multiple factors (Fisher *et al.*, 2018), and further work with bluegill sunfish and other animals is necessary to tease apart the roles of genetics, plasticity, learning or other mechanisms in shaping integrated phenotypes in individuals, populations and species. If kinematic integration is a whole-organism trait that can be acted on by selective forces, the differences among individuals might be a previously undervalued source of variation and target upon which selection on prey capture and kinematics can act in populations. For these reasons, we advocate for a complementary understanding of both physiological and functional constraints in future work aimed at understanding adaptive divergence of kinematic traits.

CONCLUDING REMARKS

The idea of coordination among parts of an organism has been prominent in biology for > 150 years, and even Charles Darwin emphasized the significance of 'correlated growth' in organisms (Darwin, 1859). However, only recently has integration of kinematic traits been suggested as a distinct area of research (Higham, 2007a, b; Kane & Higham, 2015; Kane *et al.*, 2019a). Kinematic integration may be unique, in that it is dependent on modified use of the parts and allows modulation to occur over short time spans within individuals, such as with alternative demands for prey capture. In this way, integration is mediated entirely by the need for the organism to function in its environment, making integration of kinematic traits a novel approach for understanding organism function. However, it has been unclear how behavioural modulation of component kinematic traits might affect their integration during a shared ecologically relevant task, such as prey capture.

Our work shows that integration is maintained across prey capture behaviours, despite modulation of component feeding and swimming kinematic traits, in a sample of bluegill sunfish. This consistency indicates that integration of locomotion and feeding may be a general constraint imposed by prey capture that is independent of the specific outcome used (e.g. force vs. reach suction or low vs. high swimming speed). Furthermore, individuals differ in how this constraint is manifest, such that the observed flexibility in kinematic traits is constrained within the bounds of the inflexible, individual-specific integrated relationship between traits. In this way, integration acts as an emergent functional constraint on kinematics that adds insight into variation and divergence that would not be apparent by examination of the kinematic traits of feeding or locomotion in isolation. These functional constraints are likely to act in combination with physiological mechanisms regulating the ability to coordinate motor output, and both factors are likely to play a role in governing the observed variation in kinematic traits in bluegill sunfish and in other animals that capture prey using a combination of locomotor and feeding movements. The importance of the functional constraints of integration in shaping kinematic variation represents a typically overlooked but potentially significant factor for evolution in a broad range of organisms that should be considered more directly in future studies. Our work provides a foundation for making the integration of locomotion and feeding in fishes a model system to begin to gain a better understanding of how whole organisms are shaped by complex, integrated traits.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Body size corrections.
Appendix S2. Comparing directionality of predictor and response matrices in partial least squares (PLS) analysis.
Figure S1. The role of body size on kinematic performance traits.
Table S1. Loadings from partial least squares models using alternative datasets as predictors or responses.
Table S2. Model selection statistics for partial least squares (PLS) model 1, singular axis 1.
Table S3. Model selection statistics for partial least squares (PLS) model 2, singular axis 1.

Table S4. Model selection statistics for partial least squares (PLS) model 2, singular axis 2.
Table S5. Model selection statistics for partial least squares (PLS) model 2, singular axis 3.

SHARED DATA

All videos and data representing analyzed points have been deposited in ZMAportal.org in the study 'Bluegill integration modulation' with permanent ID ZMA21. Calculated kinematic variables used in statistical analysis are available from the Dryad digital repository, doi:10.6086/D1J383 (Higham & Kane, 2020).