



SYMPOSIUM

Complex Systems Are More than the Sum of Their Parts: Using Integration to Understand Performance, Biomechanics, and Diversity

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Synopsis Organisms are comprised of many interacting parts, and an increased number or specialization of those parts leads to greater complexity and the necessity for increased integration (the ability of those parts to perform together and maintain a functioning organism). Although this idea is widely recognized among biologists, organisms are more tangibly studied when those parts are considered independently. This reductionist approach has successfully advanced our understanding of organisms’ performance. However, performance of one system might (or might not) be dependent on performance of another system to achieve a relevant outcome, and the mechanism of this dependence is poorly understood. We synthesize the concepts of complexity and integration and discuss their application in a biomechanical context. Capture of prey by predatory fishes is used as an example to highlight the application of these ideas. We provide a theoretical framework for future hypotheses of integration and predict an “integration space” for fishes that is then populated with data extracted from the literature. Additionally, using the kinematics of prey-capture in two species of sculpin (Scorpaeniformes: Cottidae), we show that species exhibit multivariate integration in distinct ways, and that these differences add additional insight into ecological divergence that would not be apparent by considering systems independently. Finally, we discuss new insights into organismal performance gained through the study of integration as an emergent property of kinematic systems working together during a common task. Integration is rarely the trait of interest, but we show that future work should adopt a more holistic approach to understand why and how animals perform complex behaviors.

Introduction

Organisms are biologically complex, being comprised of many interacting parts, including molecules, cells, tissues, organs, and organ systems. The tighter those parts depend on each other, the more integrated those parts are thought to be. In this way, integration is an emergent property of complexity (de Haan 2006), just as emotions are an emergent property of chemical interactions in the nervous system (Porges 1998; Sterck and Begeer 2010), or how flocking and schooling are emergent properties of behavioral interactions among individuals (Reynolds 1987; Viscido et al. 2004). However, many approaches to understanding organismal complexity and its importance for driving

patterns of diversity are reductionist, in which phenomena are explained as the sum of their parts, representing a “bottom-up” approach to complexity. For example, motion can be explained by understanding the activation patterns of muscles, interactions between actin and myosin, material properties of muscle and bone, and the mechanics of levers (Alexander 2003; Biewener 2003). In this way, understanding the function of each part adds insight into the integrated task of motion, although it does not provide the complete picture since one must understand how the different muscles work together.

Despite the utility of this reductionist approach for understanding how organisms function, it is

difficult to understand emergent properties that could potentially expose the system to unforeseen constraints (Korn 2005). In this way, a reductionist approach only utilizes a fraction of the available information describing complexity and inaccurate interpretations could result. For example, modifications to locomotor performance may be constrained by the ability to modify the structures and mechanisms underlying motion while maintaining an appropriate level of integration, and changes in mechanical performance may be interpreted as entirely adaptationist. However, in addition to more typical mechanical constraints that are considered, the need for integration may also provide a constraint, regulating the trajectory of diversification in mechanics (Merilä and Björklund 2004). Alternatively, more holistic approaches attempt to explain complexity using a “top-down” approach, by attempting to understand the organism and its interactions more directly. For example, performance of the locomotor system can be a factor of complex interactions between morphology, kinematics, and mechanics (McElroy and Reilly 2009) or may be constrained by other physiological systems such as reproduction (Seigel et al. 1987; Miles et al. 2000; Ghalambor et al. 2004) or feeding (Webb 1984b; Higham 2007a; McElroy et al. 2008). Despite the differences in approaches, both reductionist and holistic studies are complimentary and can be used in combination to inform each other (Nathan 2008).

One area in which reductionist approaches have been particularly prominent is in understanding the performance of organisms. Performance is the ability to execute an ecologically relevant task (Irschick et al. 2008), typically either the capture of prey or the avoidance of predators, and has been measured with a variety of techniques, including hydrodynamics, kinematics, and mechanics (Losos and Sinervo 1989; Harper and Blake 1991; Domenici and Blake 1997; Drucker and Lauder 1999; Fulton et al. 2001; Herrel et al. 2002; Walker 2004; Van Wassenbergh et al. 2007b; Wainwright et al. 2007; Holzman et al. 2008a; Tytell and Lauder 2008; Combes et al. 2010; Oufiero et al. 2011; Bates and Falkingham 2012; Marshall et al. 2012; Skorzewski et al. 2012; Rupp and Hulsey 2014). Performance-traits have been central in understanding how organisms interact with their environment due to the role of performance in explaining morphology and its relationship with fitness and survival (Arnold 1983). However, most studies have been solely interested in one system at a time (feeding or locomotion), and have taken a reductionist approach to understand how organisms carry out feeding or locomotor tasks. However, we advocate that given this extensive body of knowledge, it is now time to also consider more

holistic approaches to performance, in which feeding and locomotion might interact during a common task, adding insight into emergent constraints on these systems that would not be apparent by examining each system in isolation. In this way, whole-organism performance (e.g., success in capturing prey) might actually be defined by the ability to integrate across individual tasks (e.g., approaching prey + capturing prey), when describing each system independently might not add the level of insight gained by considering the interactions between systems.

In this article we address complexity and integration as it relates to biomechanics and performance, and use these ideas as a new way to think about how organisms function in their environment. This more holistic approach (although admittedly still reductionist to a degree) allows for novel and forward-thinking hypotheses of diversity and evolution by considering the interactions between multiple parts, and challenges the traditional boundaries of empirical research on performance. The goal of this article is to increase awareness of the importance of emergent properties, such as integration across systems at the whole-organism level, on organismal diversity and evolution, particularly for fields that are traditionally reductionist, such as comparative biomechanics. To do this, we divide the article into four aims:

- (1) To define complexity and integration and discuss these ideas from the perspective of biomechanics and performance.
- (2) To discuss the importance of integrating sub-organismal kinematic behaviors for understanding organismal diversity, using prey-capture in fishes as a model system, and provide a theoretical context for the application of these ideas.
- (3) To provide two empirical demonstrations of the integration of performance in fishes: a literature review and meta-analysis of two classical performance-traits across a diversity of fishes, and a re-analysis of previously published data using a multivariate approach.
- (4) To discuss novel insight into organismal function and performance gained by a more holistic approach, and to propose new questions to drive future research.

Complexity and integration in biomechanics

What are complexity and integration?

Complexity refers to the number of parts or layers of a system, and the greater the number of parts, the

greater the need for those parts to coordinate function (Dullemeijer 1974; Frazetta 1975; Wake and Roth 1989). In this way, interactions between the parts govern how they can be used together and therefore affect the emergent traits. However, because of variation within and between parts, emergent traits often are unpredictable (discussed in Solé and Goodwin 2000). Great effort in the physical sciences has been devoted to understanding and explaining the unpredictability that results from complexity so as to better understand emergent traits. For example, the idea that complexity in natural systems is often self-organizing until it reaches a critical point where organization fails (Bak et al. 1988; Camazine 2003) has been used to explain unpredictable phenomena such as earthquakes, extinction of species, and economic crashes (Bak 1996; Solé and Goodwin 2000; Camazine 2003), and has even been implicated to operate in conjunction with natural selection in the evolution of organisms (Solé et al. 1999; Camazine 2003). These examples highlight how complexity and the interactions among parts of a system may be an important, and overlooked, process driving biological function.

Integration is likely necessitated by complexity, and refers to the ability of parts to work together in a coordinated way (Bayliss 1921; Olson and Miller 1958; Gould and Lewontin 1979; Zweers 1979; Seaborg 1999; Pigliucci 2003). These ideas are so tightly linked that complexity and integration often are equated with each other in organismal biology (Olson and Miller 1958; Wake and Roth 1989). However, it should also be noted that the term “integration” has recently also been simplified to mean “to combine” and refers to the experimental approach of combining research methods from disparate fields to gain insight into multiple aspects of an organism simultaneously (i.e., integrative biology) (e.g., Vitousek 1990; Liem and Summers 2000; Levit et al. 2004; Holzman et al. 2008b). The interest in the current work is to address the prior meaning, in which integration describes emergent properties of biological systems.

The interest in how parts of an organism are coordinated has been prominent in biology for over 150 years, since Darwin (1859) emphasized the significance of “correlated growth”. Darwin saw integration as the correlation between two phenotypic characters, such as deafness and blue eyes in cats, and suggested that this interdependence can function independent from, but subordinate to, natural selection as a source of evolutionary change (Darwin 1859, 143, 1868; Gould 2002, 332–41). More recently, a series of univariate correlations

were interpreted as defining integrated “sets” of traits or “correlation pleiades” (Olson and Miller 1951, 1958; Berg 1960). This work established integration quantitatively as the statistical association between parts (Olson and Miller 1951, 1958; Gould and Lewontin 1979; Cheverud 1982; Wainwright et al. 2008). This idea is still in use today, with the “parts” often being functional modules (Cheverud 1982; Zelditch et al. 2004; Klingenberg 2008) such as shape of the skull (Roseman et al. 2011; Cáceres et al. 2014) or other morphological features (Klingenberg 2008). Some have even pushed this approach beyond morphological traits that are relatively fixed within an organism at small time-scales, to dynamic performance-traits (Ghalambor et al. 2003; Higham 2007b), whose integration can change given the circumstances under which the behavior is performed. This dynamic aspect of organismal integration represents a significant frontier of progress since the foundation work of Olson, Miller, and Berg 60 years ago (Olson and Miller 1951, 1958; Berg 1960).

Integration can be either passive or active (Wainwright et al. 2008) and can occur in time, space, or the interaction of time and space. Active integration results from the presence of neural processing or regulation by the organism and can be altered in response to sensory feedback, whereas passive integration lacks this component. For example, mechanical linkages and other physical properties lead to coordinated movement among parts passively, but coordinating patterns of movement across multiple joints reflects behavioral control and is therefore actively integrated (Wainwright et al. 2008). Examples of integration across time include gene regulation, in which genetic structure remains static while individual genes are sequentially expressed (Karim and Thummel 1992; Holter et al. 2000), and patterns of the activation of muscles, in which the muscle’s position is static relative to other muscles and bones but are activated in sequence to accomplish a given movement (Alexander 1991). In contrast, integration in space occurs when parts are coordinated spatially, in magnitude, or in shape. This type of integration is exemplified by morphology, when shape of the skull or body (of adults) is fixed in time but exhibits coordinated changes in shape at the population level (Klingenberg and Zaklan 2000; Peres-Neto and Magnan 2004; Bastir and Rosas 2005; Collar et al. 2014), and in the formation of proteins, when molecules are assembled and folded in a coordinated way that permits function and maintenance of shape through time (Gething and Sambrook 1992; Onuchic and

Wolynes 2004). More complex types of integration emerge with the interaction of time and space when integration is more dynamic and can change over time or with context. For example, during development and growth an organism's shape can change through ontogeny (Zelditch et al. 1992, 2006; Bookstein et al. 2003). Additionally, motion represents a form of dynamic integration, in which propulsive structures are coordinated temporally and spatially and this coordination is modulated by context (Long et al. 1994; Gardiner and Motta 2012; Falk et al. 2014; Foster and Higham 2014). It is also important to note that dynamic forms of integration may also involve learning, in which the level of integration can change with experience, such as with predatory fishes learning to coordinate attack-and-strike behaviors to capture prey (Coughlin 1991; Wintzer and Motta 2005; Reid et al. 2010; Lönnstedt et al. 2012). Distinguishing the dimension on which integration occurs allows for a better understanding of the phenomena and a more informed empirical application of the concept.

The role of integration in organismal performance

Studies of organismal diversity are common in comparative biomechanics, where questions often are centered on the morphology–performance–fitness paradigm popularized by Arnold (1983). Performance refers to the ability to perform an ecologically relevant task (Irschick et al. 2008), and has been quantified using kinematics such as acceleration during escape from predators (Law and Blake 1996; Walker et al. 2005; Herrel and Bonneaud 2012) or mechanics such as bite-force during the capture of prey (McBrayer 2004; Herrel et al. 2005; Huber et al. 2005; Marshall et al. 2012). Although some researchers have examined direct links between performance and fitness (e.g., Jayne and Bennett 1990; Walker et al. 2005; Husak 2006; Langerhans 2009), measuring fitness associated with biomechanical traits in the field is difficult, and other researchers have focused on the relationship between morphology and performance instead (Webb 1978; Walker and Westneat 2002b; Blake 2004; Carroll et al. 2004b; Wainwright et al. 2007; Domenici et al. 2008). Because of its central role in explaining organismal form and the expectation of evolutionary consequences, performance has played a central role in comparative biomechanics, in which differences at this level are used to characterize differences in both morphology and fitness.

Although performance has been useful for adding insight into differences between and among species,

studies tend to reduce organismal complexity to individual functional systems, such as locomotion or feeding and performance refers to a relevant outcome of either system. However, a more holistic idea is that organisms result from integrated levels of complexity (Bayliss 1921; Olson and Miller 1958; Gould and Lewontin 1979; Zweers 1979; Seaborg 1999; Pigliucci 2003), and systems can work together to perform a common ecologically relevant task. Because parts do not often function independently, significant aspects of evolutionary change can be overlooked when these systems are considered separately (Olson and Miller 1958; Zweers 1979). In fact, the correlated function of parts may be more beneficial for understanding organismal evolution than is understanding the function of the individual parts because it provides insight into mechanisms of constraint (Bayliss 1921; Gould and Lewontin 1979). In a recent review of selection on performance-traits, Irschick et al. (2008) highlight that future work should assess selection on multiple traits, given that performance does not evolve independently from other features of the organism. However, little research has been devoted to addressing multiple interacting traits and many studies still use “performance” to refer to system-level traits. However, the relevant outcomes of each system are not likely additive when implemented in combination, but rather comprise a tradeoff that must be mitigated during integrated behaviors (Ghalambor et al. 2003, 2004; Irschick et al. 2008; Walker 2007, 2010). In this case, neither measure of system-level performance adequately describes the emergent level of organismal performance achieved when both systems act together.

Therefore, we argue that examining integration of system-level traits during a common, ecologically relevant behavior not only addresses concerns of multiple interacting systems, but also quantifies an emergent level of performance that is only apparent when systems work together. For example, knowing how much suction an animal can generate (traditionally, a measure of feeding performance) does not necessarily inform whether that animal will actually capture the prey. Instead, the successful capture of prey likely reflects multiple factors, including both the ability to position the mouth relative to the prey as well as the ability to generate the appropriate suction forces (Wainwright et al. 2001; Higham et al. 2006a; Kane and Higham 2014). Not only can the appropriate force vary with the type of prey (Holzman et al. 2008b, 2012), but accuracy and suction may not be synergistic (Kane and Higham 2014). Therefore, we instead use the term

“performance” to refer to ecologically relevant tasks at the organismal level, such as the capture of prey, which often rely on more than one system. In this way, integration is itself an emergent measure of performance that describes the kinematic behavior of each system as systems work together. Thus, kinematic integration is similar to behavioral integration (i.e., behavioral syndromes) (Sih et al. 2004) in that kinematic integration occurs at the organismal level, and can likely change each time the behaviors are executed. However, kinematic integration involves motion of structures and therefore represents integration across the dimensions of time and space, whereas behavioral integration doesn't necessarily involve spatial changes. Kinematic integration is also similar to types of functional integration, i.e., sensory-motor (Johansson and Cole 1992; Vicario 2004) in that both reflect a cooperative function of systems. However, functional integration is typically sub-organismal and less subject to voluntary control compared with kinematic integration. Therefore, for the remainder of this manuscript, we use the term “integration of kinematics” to refer to dynamic kinematic behaviors that are voluntarily coordinated during a common task, and can be used as a more holistic and ecologically or evolutionarily relevant measure of organismal performance.

Although integration of kinematics as an organism-level metric is a relatively new approach (Higham et al. 2005, 2006a; Higham 2007a, 2007b), a large body of work has centered on integration of morphological traits. The interest has been in the mechanism and variability of morphological integration, as well as in the evolutionary implications (Peres-Neto and Magnan 2004; Badyaev et al. 2005; Marugán-Lobón and Buscalioni 2006; Collar et al. 2008; Mitteroecker and Bookstein 2008; Porto et al. 2009; Klingenberg et al. 2011). This extensive effort has led to methodological advances in quantifying integration as multivariate phenomena within and across taxa (Rohlf and Corti 2000; Adams and Felice 2014), and has demonstrated that integration among morphological traits is readily apparent (reviewed in Klingenberg 2008). This work has been important for establishing the role of morphological integration in describing differences among organisms and their evolutionary trajectories. However, if selection acts on behavior and morphological changes are indirect (Garland 1994; Garland and Losos 1994), then the ability for organisms to integrate behaviors in a meaningful way during ecologically relevant tasks may be more important for understanding the factors governing survival and evolution of organisms (Irschick et al. 2008).

Additionally, significant advancements in the understanding of functional mechanisms within systems make it possible to begin examining interactions between systems. For this reason, questions of correlated interactions among functional traits at the sub-organismal level have recently become of interest (Rice and Westneat 2005; Higham 2007a; McElroy et al. 2008; Rice 2008; Montuelle et al. 2009, 2012b; Oufiero et al. 2012; Bimbard et al. 2013). Therefore, the success of morphological integration and the growing interest in interactions among functional systems suggest that it is a perfect time for challenging researchers to think about organismal performance in a new and integrated way.

Quantifying integration

Integration represents the pattern of biological covariation (Pigliucci 2003), and can be quantified statistically by the correlation coefficient between functional units (Olson and Miller 1951, 1958; Gould and Lewontin 1979; Cheverud 1982; Zelditch et al. 2004; Klingenberg 2008; Wainwright et al. 2008). Some investigations of integration have used alternative metrics, such as coefficient of variation (Rice and Westneat 2005; Rice et al. 2008), but this addresses repeatability of functional units rather than coordinated changes between functional units. Additionally, functional units themselves have been described in varying ways, from using univariate comparisons of individual kinematic or morphological variables (Higham 2007a, 2007b; Higham et al. 2007; Kane and Higham 2011; Oufiero et al. 2012) to multivariate comparisons of suites of variables (Lauder 2000a; Collar et al. 2008; Rice 2008; McElroy and Reilly 2009; Montuelle et al. 2009, 2012a). However, univariate analyses may not capture complex relationships among traits, and to date, multivariate analyses have only been able to indirectly assess the covariation between datasets (Mevik and Wehrens 2007).

A promising statistical technique for assessing multivariate covariance that is widely used in studies of morphological integration (Klingenberg and Zaklan 2000; Rohlf and Corti 2000; Zelditch et al. 2004) and other diverse research areas (Wold et al. 2001; Boulesteix and Strimmer 2007; Carrascal et al. 2009; Qureshi and Compeau 2009; Krishnan et al. 2011) is partial least squares (PLS). This ordination technique is similar to others such as principal components analysis (PCA) in that it is a method of data reduction. The exception is that PCA describes the variance present in only one dataset whereas PLS describes the covariance between two

datasets. It does this by extracting singular axes (SA; analogous to principal component axes) that describe the latent patterns underlying the covariation between datasets (Wold 1975; de Jong 1993; Garthwaite 1994; Wold et al. 2001; Haenlein and Kaplan 2004; Zelditch et al. 2004; Mevik and Wehrens 2007; Abdi 2010). These axes are related back to the original samples using scores on each SA (analogous to principal component scores) and like PCA, the subsequent latent variables describe the remaining portion of the variance that was not captured by the prior axes, and all axes are orthogonal. A difference, however, is that each SA is composed of pairs of scores that relate to one or the other of the original data matrices (Fig. 1). In this way, scores for SA1 for example would describe an axis of predictors that maximally explains the variation in responses, and vice versa. Following ordination, axes can then be correlated or regressed to determine the statistical association between datasets (Zelditch et al. 2004; Abdi 2010; McGuire 2010). In this way, PLS coupled with correlation or regression represents a similar analytical approach as that of traditional univariate analyses (e.g., Higham 2007a, 2007b; Higham et al. 2007; Wainwright et al. 2008; Kane and Higham 2011) but the axes are multivariate and the approach to summarizing the covariation is more direct. For this reason, PLS correlations provide a useful statistical test for assessing integration between multiple variables simultaneously, and we advocate its adoption into studies of interactions among multiple traits.

Understanding integration using the capture of prey by fishes

Fishes as a study system

Fishes are an exceptional system for examining integration of kinematic traits given that locomotion and feeding have been studied extensively in independent contexts (Harris 1936; Liem 1978; Lauder 1982, 2000b; Webb 1982b; Motta 1984; Wainwright 1996; Domenici and Blake 1997; Wainwright and Shaw 1999; Westneat et al. 1999; Walker and Westneat 2002a; Wainwright et al. 2002, 2007; Blake 2004; Dean et al. 2007), thereby providing a broad body of knowledge to begin forming working hypotheses of integration. Integration between locomotion and feeding is expected because fishes have a greater degree of movement in both systems due to a greater number of control surfaces (fins) for locomotion and highly kinetic skulls (related to feeding) compared with other vertebrates, necessitating integration to a greater degree due to the greater number of

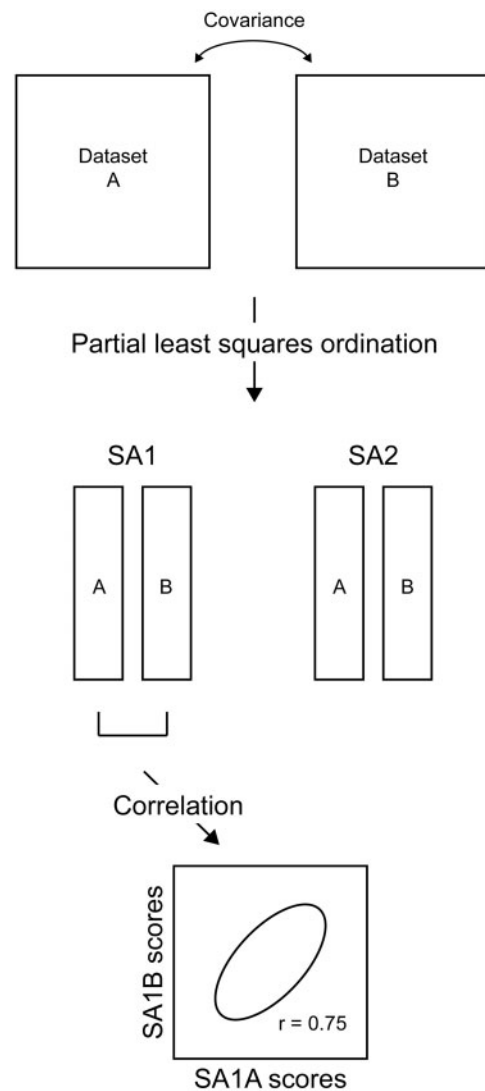


Fig. 1 An illustration of the work flow of PLS correlation analyses. The covariance between two multivariate dataset matrices is summarized using PLS, yielding potentially multiple SA vectors that describe this covariance. Each SA has two components that correspond to each original multivariate dataset. The scores on these components can then be related using a correlation between them (shown using a 95% confidence ellipse), where the statistic (r) represents the association between the datasets, or integration.

interacting parts (Dullemeijer 1974; Wake and Roth 1989). Also, the mouth is only useful for capturing prey at close distances, often necessitating a reliance on locomotion to approach prey prior to capture (Webb 1984b; Wainwright et al. 2001; Higham 2007b). However, locomotor and feeding systems are relatively modular in fishes (although there is evidence for some overlap) (e.g., Camp and Brainerd 2014) and can be used separately with success (e.g., a fish can swim without opening its mouth), indicating that integration likely results

entirely from functional co-dependence (Wainwright et al. 2008). This is in contrast to integration being the direct result of shared developmental or neural pathways (e.g., in taxa that use the same structure for both behaviors) (Altenbach 1989; Nekaris and Rasmussen 2003), cause–effect relationships, or mechanical linkages (Wainwright et al. 2008), where the integration may or may not have the ability to change across contexts.

Not only is integration expected in recent studies and supported by them (Higham 2007a, 2007b; Kane and Higham 2011; Oufiero et al. 2012), modulating the kinematics both of attack and feeding (Nemeth 1997; Ferry-Graham et al. 2001; Van Wassenbergh and De Rechter 2011; Gardiner and Motta 2012; Kane and Higham 2014) suggests that integration may also vary depending on context. Aquatic predators can modulate the patterns of activation of feeding muscles (Wainwright and Lauder 1986) and kinematics (Anderson 1993; Lemell and Weisgram 1996; Matott et al. 2005; Van Wassenbergh et al. 2006; Van Wassenbergh and De Rechter 2011) in response to type of prey. Some fishes swim faster when their prey are more evasive (Nemeth 1997; Ferry-Graham et al. 2001) so that prey have less time to escape (Higham 2007b). Modulation of integration may be apparent either by a change in the magnitude (high versus low) or pattern (components, which parts are coordinated) of integration. However, traits are likely modulated along a continuum related to trade-offs. For example, during the capture of prey, strong suction often is observed during slow swimming and vice versa (Nyberg 1971; Higham et al. 2006a; Oufiero et al. 2012), and integration likely represents an emergent level of performance that is not apparent by studying each system in isolation (Kane and Higham 2011). In this way, a balance must be achieved between these complex systems in order to maximize the overall success of the event. Because differences in performance can occur from trial to trial, integration between locomotion and feeding in fishes represents not only dynamic integration of parts across time and space, but changes in integration can occur at very rapid time-scales, and fishes are a practical system for addressing responses to changing environmental conditions.

Diversity in locomotion and feeding

Given the diversity of almost 33,000 described fishes (Fishbase: Froese and Pauly 2014), it is reasonable to expect large variation both in locomotion and feeding across fishes. However, these behaviors can be

distilled into common performance modes according to the contribution of functional components (i.e., moving parts) to each behavior (Fig. 2). These performance modes then allow for more tangible comparisons between modes and across performance-systems. Here, modes of locomotion and feeding are used to hypothesize potential links or constraints across modes, allowing for large-scale predictions of the effect of integrated traits on patterns of diversity in fishes to be generated.

Locomotor modes during capture of prey can be defined according to whether or not a translation of the body's position is observed, and if so, which parts of the body generate this movement (Webb 1982b, 1984b). Some fish use alternative means to encourage prey to approach on their own, negating the use of locomotion to approach the prey (e.g., anglerfish of the Order Lophiiformes that use a modification of the first dorsal fin ray as a lure, or stonefish of the Order Scorpaeniformes that rely on camouflage to hide from prey). However, this is a specialized strategy, and it is more likely that a majority of fishes approach their prey prior to capture. Predators that pursue prey rely primarily on median and paired fins for maneuvering around objects (Higham 2007a, 2007b) or body and caudal fins to pursue prey at a sustained velocity (Nyberg 1971; Webb 1982a, 1984a) or with a high-acceleration lunge (Webb and Skadsen 1980; Webb 1982a, 1984a). However, these locomotor modes may not be mutually exclusive, as fish can modulate the number and type of fins used with changes in speed (Drucker and Jensen 1996; Korsmeyer et al. 2002; Jagnandan and Sanford 2013) or context to employ a generalist strategy.

Modes of feeding similarly can be described by the contribution of functional components leading to expansion of the mouth (Fig. 2). Ram feeders rely primarily on expansion of the gape and on forward velocity to overtake planktonic prey (Rosen and Hales 1981; Tomita et al. 2011), small prey (Muller and Osse 1984; Van Leeuwen 1984) such as aquatic insects, or large prey such as other vertebrates (Lauder and Liem 1981; Frazzetta and Prange 1987). However, note that some ram predators may also use expansion in other dimensions (Lauder and Liem 1981). Predators that use biting to capture prey rely primarily on gape and on protrusion of the jaw to scrape and remove sessile prey (Rice 2008; Rupp and Hulsey 2014), to pick small individual prey from the water column (Gibb et al. 2008; Copus and Gibb 2013), or to remove pieces from large prey (Tricas and McCosker 1984). Finally, suction-feeders rely on rapid expansion in all three dimensions to generate

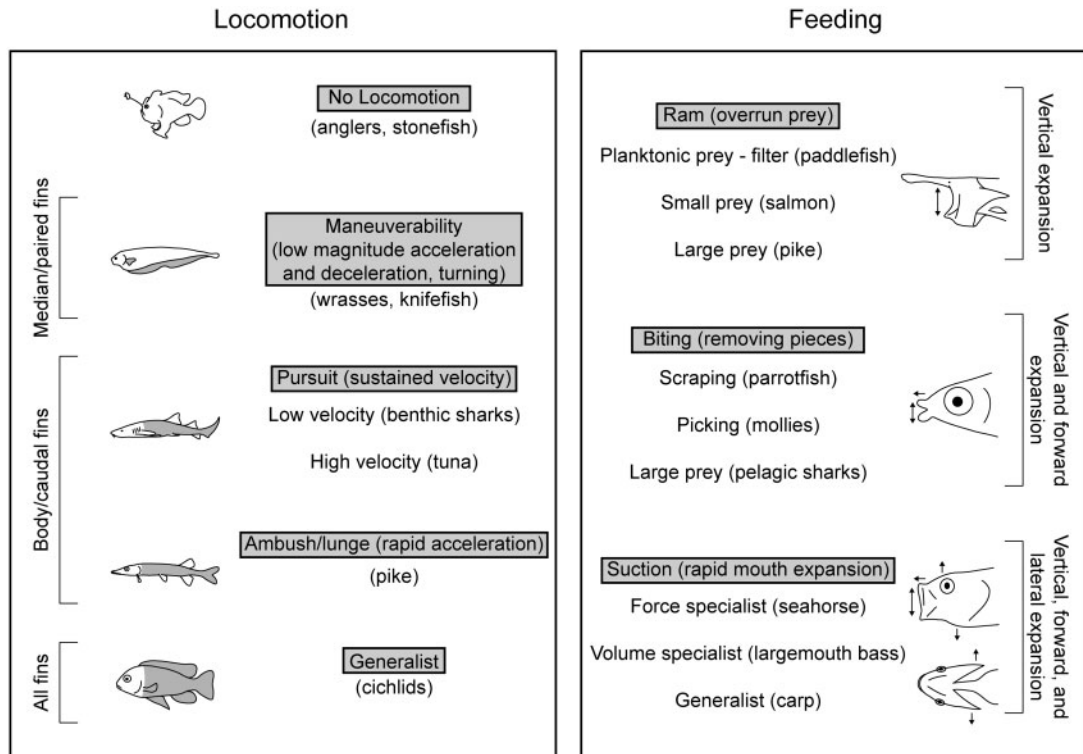


Fig. 2 Modes of locomotion and feeding during the capture of prey by fishes. Representative taxa exemplify each mode. Modes vary in the contribution of functional components (i.e., moving parts) within each system. Locomotor components are shaded in gray; feeding components are shown with arrows.

hydrodynamic forces that draw prey toward the predator (Muller et al. 1982; Muller and Osse 1984; Day et al. 2005, 2007; Holzman et al. 2008b). Within suction, fish can generate rapid flow of water and strong forces by coordinating the timing of the feeding movements (Holzman et al. 2007; Bishop et al. 2008), they can generate large ingested volumes by modulating the magnitude of the mouth's expansion (Higham et al. 2006a), or they can use a combination of these techniques to employ a generalist strategy (Nyberg 1971; Muller and Osse 1984). Suction often is considered to be the most common method of capturing prey in aquatic vertebrates (Lauder 1985), and the prevalence of this method may be due to the ability to combine other feeding modes with suction (Norton and Brainerd 1993; Ferry-Graham et al. 2002) so that these modes are not mutually exclusive. Additionally, as with locomotion, many fishes may be capable of multiple modes of feeding and can modulate depending on the context (Nyberg 1971; Anderson 1993; Lemell and Weisgram 1996; Nemeth 1997; Ferry-Graham et al. 2001; Matott et al. 2005; Van Wassenbergh et al. 2006; Van Wassenbergh and De Rechter 2011; Kane and Higham 2014). By defining potential modes of locomotion and feeding in fishes, combinations of modes

that may be more or less common become more apparent and hypotheses of constraint can be formed.

Integration as an axis of diversity

Although studies have considered the role of locomotion in the capture of prey (Webb and Skadsen 1980; Rand and Lauder 1981; Van Leeuwen 1984; Webb 1984a, 1984b), direct studies of integration between these two systems are few. For this reason it is helpful to generate a paradigm under which predictions can be made and hypotheses can be tested so that future research can be guided by a unifying theory. The work discussed above provides a foundation that allows us to begin to formulate such a theory to describe one potential axis of diversity in fishes that accounts for traits of locomotion and feeding simultaneously. To do this, we hypothesize an "integration space" using two traditionally important variables to predict the influence of integration on fish diversity (Fig. 3). This integration space predicts the relationships between locomotor and feeding modes, the strength of integration between modes, and the composition of variables contributing to integration between modes (as a result of the functional components driving each mode)

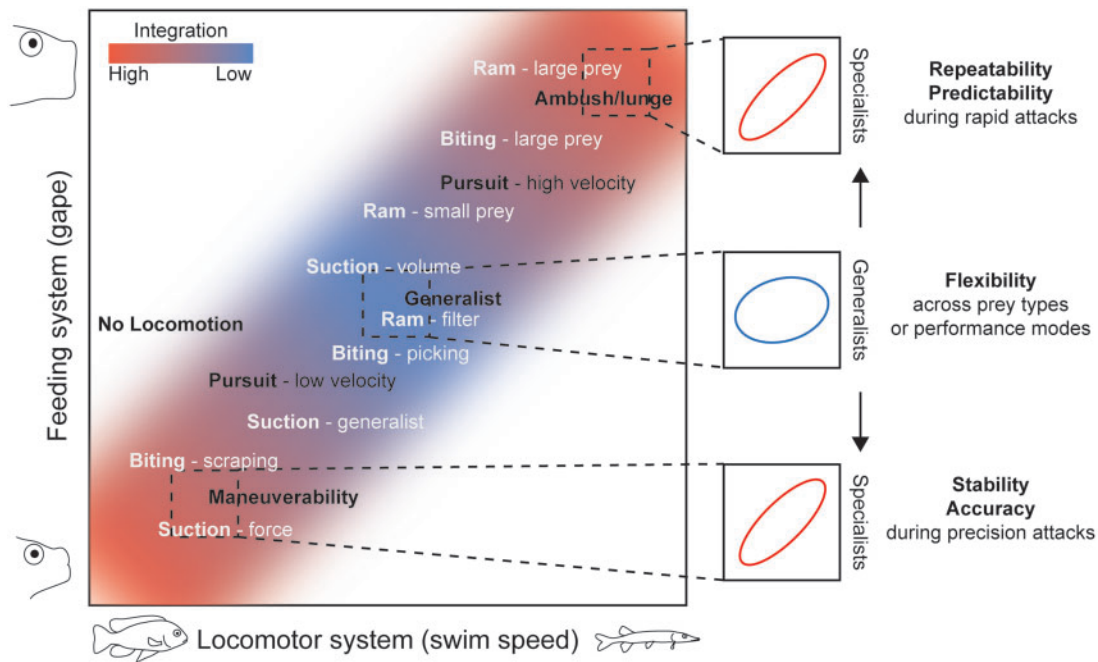


Fig. 3 A proposed “integration space” demonstrating integration between locomotion (black) and feeding (white) during the capture of prey by fishes. The space is defined by the gape and swimming speed (ram) of the predator because these traits are traditional drivers of each system. Proximity of locomotor and feeding modes indicates a stronger association, so that some modes are more likely to occur in combination (e.g., force-specialized suction and maneuverability). Alternatively, more distant modes (e.g., force-specialized suction and high-acceleration lunge) are less often associated. Color indicates the strength of integration between systems (red, high; blue, low). Integration, or correlation, is likely stronger in specialists at the extreme ranges and provides an advantage in either repeatability or predictability during rapid strikes, or stability and accuracy during more precise strikes. Alternatively, integration is likely weaker when the need for flexibility across modes and prey types may be greater.

(Fig. 2) that can be used to validate the role of integration in patterns of diversity and evolution. If understanding how parts work together is important for understanding evolutionary change, as suggested (Bayliss 1921; Olson and Miller 1958; Gould and Lewontin 1979; Zweers 1979), then analyses of patterns of integration among functional kinematic-traits represent a novel and important area of progress.

To construct the integration space, variables thought to be primary drivers of the relevant outcome of each system were used. Peak gape and ram at peak gape (Higham 2007a; Higham et al. 2007; Oufiero et al. 2012; Kane and Higham 2014), or morphological traits directly related to these abilities (Higham 2007b; Collar et al. 2008) have been the primary variables used to represent locomotion and feeding in fishes during an integrated behavior such as capture of prey. These two variables also have been strong contributors to multivariate performance (Kane 2014; this study), indicating the importance of their role. Within these axes, hypothesized locations of modes were plotted (Fig. 3). This visualization

demonstrates a number of important features of integration and how this emergent level of performance might vary across fishes. First, the relative distance of modes indicates the likelihood of association, where modes that are closer in space likely occur together more frequently (i.e., ambush/lunge with ram for large prey). These types of associations also reflect potential tradeoffs, so that modes that are more distant cannot be performed at the same time (i.e., forceful suction and ram for large prey). Finally, these associations suggest that, for some modes, there may be several options for integration (generalist locomotion with volume-specialized suction, filter-feeding ram, or biting/picking). A second important prediction is that, because of these associations, prey-capture itself may be integrated, so that a change in one system results in a corresponding change in the other system. Therefore, by considering use of both systems simultaneously, an additional layer of constraint upon traits is apparent that has seldom been considered previously.

In addition to demonstrating likely associations between modes, the integration space also

demonstrates hypothesized differences in the magnitude of integration (strength of the correlation between traits) according to the degree of specialization along each axis (Fig. 3, shaded areas). Specialization may require tighter integration between locomotion and feeding (Webb 1982b), either because of a greater need for systems to work together, or simply because there are a constrained number of options available to predators (Webb 1984b; Higham 2007b; Kane and Higham 2011). For example, predators that approach at high speed increase integration of patterns of muscular activity and kinematics within the feeding system (Liem 1978; Oufiero et al. 2012), as well as between peak gape and velocity of swimming at the time of peak gape (Higham 2007a). Higher integration between locomotion and feeding during specialized attacks, when gape is large and the speed of swimming is fast, may provide an advantage when little time is available to make decisions regarding the capture, thereby ensuring a repeatable and predictable strategy of attack. Alternatively, for predators whose gape is small and ram is slow, the reliance on suction and decelerating prior to capture of the prey may be greater (Higham 2007a), and increased integration could facilitate increased stability and accuracy of the strike (Kane and Higham 2014). This idea is supported by an observed increase in integration, accuracy, and success in predation attempts by bluegill sunfish (*Lepomis macrochirus*) when capturing non-evasive prey and using smaller gapes and slower speeds of swimming (Kane 2014).

However, specialists at either end of the integration-space may be at a disadvantage relative to generalists because specialization limits flexibility of the components of integration. This inflexibility could also limit the ability to rapidly change integration in response to the prey's behavior or other factors. The inflexibility of specialists is also supported by data from bluegill that demonstrate reduced integration, accuracy, and success of capturing evasive prey, and that ultimately lead to larger gapes and faster ram-speeds for capture (Kane 2014). Alternatively, the integration-space predicts that a predator with more generalized traits, such as largemouth bass (*Micropterus salmoides*), which are suction-volume specialists that use high velocity pursuit, would demonstrate a weaker magnitude of integration, but greater flexibility in integration (components contributing to integration). Although integration has yet to be determined for this species, largemouth bass exhibit similarities in accuracy and success of capture across divergent types of prey (Kane and

Higham 2014), supporting at least a portion of this hypothesis.

Together, the complexity of factors contributing to observed differences in integration are likely useful for regulating the tradeoffs between and among strategies, and understanding the mechanisms and variability of integration are important first steps toward understanding how organisms perform and survive in their environment. To demonstrate the importance of integration in understanding constraints and diversity, the following two analyses are performed below: (1) a meta-analysis of data describing ram and gape that were available in the literature is plotted to begin to test hypotheses presented in the integration-space, and (2) a dataset of kinematics describing locomotion and feeding (Kane and Higham 2011) are re-analyzed using PLS to demonstrate a new mechanism of analyzing and interpreting organism-level integration of kinematics. Finally, these results are discussed in terms of the insights gained by assessing performance as an emergent property of integration between sub-organismal functional traits.

Demonstrating integration of kinematics

Meta-analysis of ram and gape

To assess the predictions presented by the integration-space (Fig. 3), values of maximum gape and of the velocity of the predator (ram) for several species were taken from the literature (Supplementary Table S1). Surprisingly, only 20 studies reported both of these values, which may be explained by the fact that most investigators of feeding are not interested in the predator's velocity and most investigators of locomotion are not interested in the size of the predator's mouth. Of these 20 studies, two represented a phylogenetic approach encompassing 18 or more species (Higham et al. 2007; Oufiero et al. 2012) and two represented a comparative approach offering multiple types of prey to at least three species (Wainwright et al. 2001; Kane 2014). Together, these studies represent a diversity of species and strategies for capturing prey, ranging from more basal forms such as pickerel, gar, cod, and trout to more derived forms such as seahorses, eels, centrarchids, cichlids, and serranids. Individual sizes ranged from 2.85 to 60.9 cm total or standard length, depending on the study, and due to these differences in measurements, individual size was not taken into account in the analysis. However, size did not appear to significantly affect the relationship between ram and gape since larger and smaller individuals occurred throughout

the space. For example, one of the fastest species, *Caquetaia kraussii*, was only 8.3 cm in length and the largest species, *Anguilla rostrata*, swam at only 27 cm/s (Supplementary Table S1). Across the studies that reported ram, these data were measured differently so comparisons should be made with caution. For example, some studies simply reported a velocity without mention of whether it was peak velocity, mean velocity, or velocity at peak gape, and whether it was for a single trial or an average across trials. Six studies reported correlations between ram and gape (Higham et al. 2006a, 2007; Tran et al. 2010; Kane and Higham 2011; Oufiero et al. 2012; Kane 2014), supporting integration, but patterns relating to the integration-space were not apparent. This could be because ram was calculated differently across studies or because integration may be more of a multivariate phenomenon and could not be captured well using only two variables (see re-analysis of the data for sculpins below).

This meta-analysis of values of ram and gape reported in the literature demonstrates a correlation between the two variables across species, as predicted (Fig. 4A). This trend can be highlighted by two extreme examples. Syngnathiformes (including seahorses and pipefishes) are well known for their forceful suction (Muller and Osse 1984; Bergert and Wainwright 1997; Van Wassenbergh et al. 2009). These fishes use low-speed maneuvering via undulations of the dorsal fin to approach prey, and the combination of low speed during ram and a small gape (Muller and Osse 1984) places them in the lower left corner of the integration-space, as predicted. Alternatively, rainbow trout approach prey at high, sustained velocity and rely mostly on ram to capture small prey (Van Leeuwen 1984). Their resulting large gape (Van Leeuwen 1984) places this species at the upper right corner of the integration space where the corresponding locomotor and feeding modes are predicted to occur. Finally, the prediction that locomotor and feeding modes change predictably is supported by a correlation across species ($r=0.66$, $P=0.0023$). Although studies collected and reported data in varying ways, and the data shown here were not corrected for size or phylogeny, a strong correlation between these two traits indicates that this relationship is likely significant.

For a few species of fishes, data were available in replicate across prey-types within the same study, in which methodology and measurement were similar between treatments and allowed for a comparison of variation in integration within species. When data from these studies are plotted separately

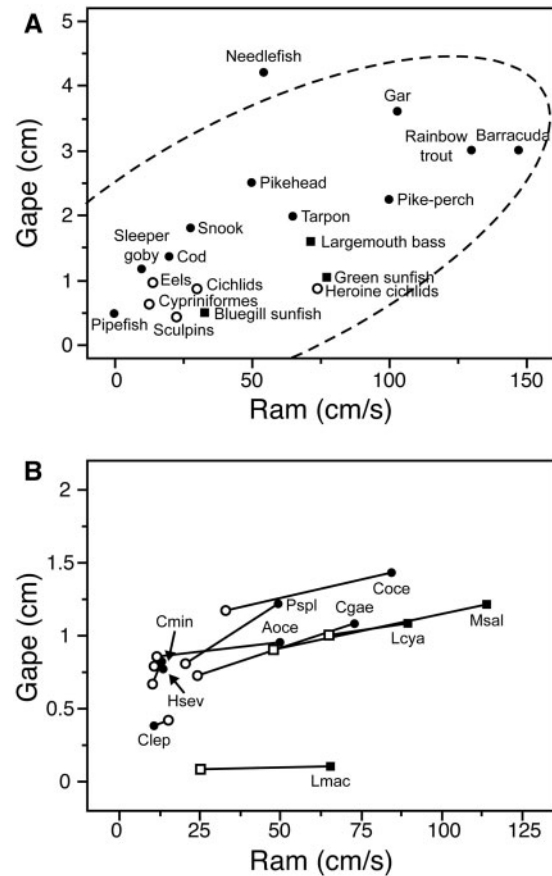


Fig. 4 Testing the predictions of the integration space (Fig. 3) data extracted from the literature (Supplementary Table S1). Values have not been corrected for the predator's body size (because "size" is reported using different measurements across studies) or for phylogenetic relationships. (A) Values are for each species (filled shapes) or higher taxonomic groups (open shapes), and sunfish species shown in detail in panel B are shown with filled squares. Where multiple studies provide replicate data, means are shown. A correlation is observed across taxa ($r=0.66$, $P=0.0023$) and is shown using a 95% confidence ellipse. (B) Species for which the same study assessed ram and gape across two types of prey (open, non-evasive; filled, evasive). Species' names are abbreviated using the first letter of the generic name and the first three letters of the specific epithet (Supplementary Table S1), and are placed near the marker for the evasive prey. Means for the same species are connected with a line to signify a range of performance space occupied. Within-species variation mimics across-taxa variation for most species.

(Fig. 4B) it suggests that variation within a species can be quite large and mimics the pattern observed across all taxa. For example, largemouth bass (Msal) exhibit the greatest distance between prey-types, whereas severum cichlids (Hsev) have the smallest. Additionally, all species appear to have a positive slope, but the magnitude varies from nearly horizontal in bluegill (Lmac) to nearly vertical in Minckley's cichlid (Cmin). These differences suggest a

correlation between ram and gape during capture of prey, but that the variation in each performance-measure, and therefore the effect on integration, likely differs across species. Interestingly, the species with the most restricted ability to modulate variables are those with zooplanktivorous or herbivorous diets (Wainwright et al. 2001), which may represent more specialized behavior and which supports the hypothesis that integration in specialists may be a factor of the limited number of options available. It is important to note also that for studies that examined the relationship between ram and gape across a phylogenetic sample (Higham et al. 2007; Oufiero et al. 2012) the relationship is given in the respective papers and is not replicated here, although positive correlations were observed in both cases, further reflecting the integration-space. Despite the limiting sample sizes and differences across experimental methods, these data (Supplementary Table S1) are still useful because they provide an example of the potential performance-space a species or group of species might occupy. Overall, the results of this meta-analysis indicate that the hypothesized performance-space (Fig. 3) summarizes species diversity well and stimulates further questions into variation within and among species, and how that might also be important for driving diversity.

Multivariate integration in sculpins

To provide an example of a multivariate analysis of integration using PLS, and to demonstrate the utility of this type of analysis for understanding variation within and between closely-related species, previously published data on locomotion and feeding for two species of sculpins (Kane and Higham 2011) were re-analyzed. Whereas tidepool sculpins (*Oligocottus maculosus*) are more typical of sculpin morphology and behavior, using specialized locomotor morphology to maintain position on the substrate in flow (Webb et al. 1996; Taft et al. 2008; Kane and Higham 2012), silver-spotted sculpins (*Blepsias cirrhosus*) are relatively less specialized fishes that swim more constantly. However, both species are similar in the size of their mouth and their use of suction during feeding (Kane and Higham 2011). Therefore, these species were used to assess differences in univariate integration between kinematic-traits due to specialization of the locomotor system (Kane and Higham 2011).

Descriptions of the kinematics, representative kinematic traces, and previous results are described elsewhere (Kane and Higham 2011) and are not repeated here. Size-corrected data were broken into

two datasets: the dataset representing feeding included peak gape, time to peak gape, peak cranial elevation, time of peak cranial elevation, and peak protrusion of the upper jaw; the dataset representing locomotion included the initial distance between predator and prey, predator-prey distance at opening of the mouth, peak velocity, time of peak velocity, peak acceleration, time of peak acceleration, peak deceleration, time of peak deceleration, and velocity at peak gape. Not all variables describing movement of the predator were included in re-analysis because these are not included in other studies. Additionally, not all potential variables related to feeding were included in the previous study (i.e., hyoid depression), and therefore they are not included here. A PLS ordination was performed using locomotor variables as the predictor and feeding variables as the response (due to the time-dependence of the events) and a correlation between components of each significant SA was used to determine integration. Correlation is preferred over regression because there is no assumption of one axis predicting another.

Previously, silver-spotted sculpins were concluded to have stronger integration than tidepool sculpins due to the slightly greater number of variables that displayed a univariate correlation (Kane and Higham 2011). However, multivariate analysis determined that two SAs describe integration between these species, and on the first axis both species are similar whereas on the second axis tidepool sculpins have approximately 30% stronger integration (Fig. 4), reversing the conclusions of the previous study. Additionally, multivariate correlations were generally stronger than univariate correlations, suggesting a greater ability to capture covariation with a multivariate analysis. Combined, the multivariate model explained 58.8% of the variation in locomotion and 45.8% of the variation in feeding. These low values may be due to the exclusion of variables as described above.

The complexity of integration in these two species is highlighted not only by two axes of integration, but also by differences in the variables driving those axes. The first axis (Fig. 5A), upon which both species have similar correlations and therefore integration, represents integration between translation of the body and volume of the mouth. In this case ram and gape are the driving factors of integration. However, on the second axis (Fig. 5B), timing becomes more important for both datasets and this axis represents integration between feeding strategies (strong or weak suction) and locomotor strategies (early acceleration for close prey or late acceleration

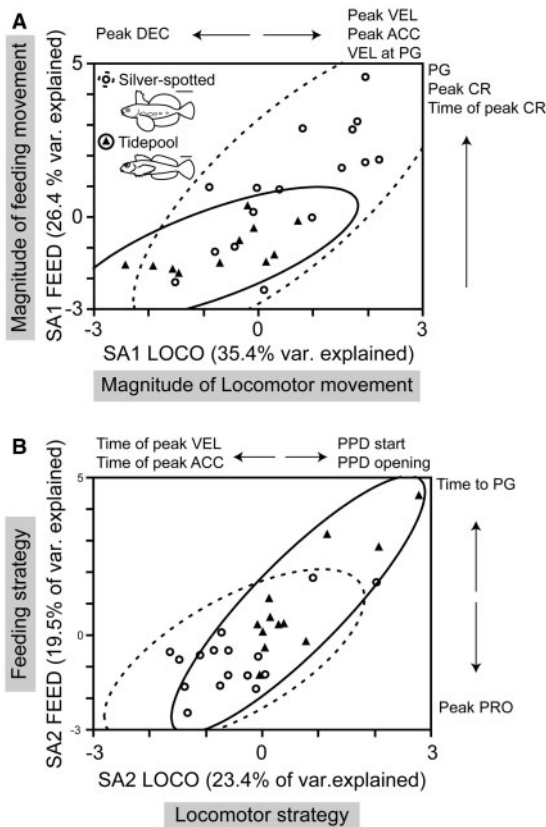


Fig. 5 Results of PLS correlation between locomotor (LOCO) and feeding (FEED) variables. **(A)** The first axis describes integration between the magnitudes of locomotor and feeding movements, where the positive directions represent larger intraoral volume and faster approach speeds on the X- and Y-axes, respectively. Both species show similar integration on this axis (silver-spotted $r=0.765$; tidepool $r=0.724$). Scale bar is 1 cm. **(B)** The second axis describes integration between locomotor and feeding strategies, accounting more for differences in timing of events. Here, the positive direction represents weaker suction force and acceleration that occurs closer to the time of prey capture when prey initially are located farther from the predator. *Oligocottus maculosus* displays stronger integration than *Blepsias cirrhosis* on this second axis (silver-spotted $r=0.672$; tidepool $r=0.875$), indicating that differences between species are apparent in integrating locomotor and feeding strategy, rather than simply integrating locomotor and feeding magnitude. ACC acceleration; DEC deceleration; CR cranial elevation; PG peak gape; PPD predator-prey distance; PRO upper jaw protrusion; var variation; VEL velocity.

for distant prey). It is in this case that tidepool sculpins have stronger integration. These two integration axes suggest that the relationship between ram and gape is a primary driver of integration to which both species have to accommodate similarly. However, finer-scale differences between species may come from the contribution of additional variables and how they relate to the specializations or behaviors

of each species along secondary axes of integration. For example, the morphological specialization of the locomotor system in tidepool sculpins may contribute to a need for increased integration, supporting the role of specialization in integration (Webb 1982b, 1984b; Higham 2007b; Kane and Higham 2011). Alternatively, *Blepsias cirrhosis* lacks most of this morphological specialization of the pectoral fins (Kane and Higham 2012) and also displayed weaker integration on a secondary axis. This analysis demonstrates the complexity of performance-integration and how a multivariate approach is necessary for describing subtle nuances in differences between species. For this reason, we suggest that future analyses of integration should consider a multivariate approach.

New insights and future directions

While it is generally understood that organisms are complex, many approaches to organismal function are understandably reductionist, and attempt to understand function within parts rather than across parts (e.g., Losos and Sinervo 1989; Bels et al. 1997; Domenici and Blake 1997; Wakeling and Johnston 1998; Drucker and Lauder 1999; Motta et al. 2002; Sanford and Wainwright 2002; Lauder and Tytell 2005; Van Wassenbergh et al. 2005; Blake 2006; Higham et al. 2006b; Deban et al. 2007; Mehta and Wainwright 2007; Ferry-Graham et al. 2008; Roos et al. 2009; Combes et al. 2010; Kane and Higham 2012; Camp and Brainerd 2014). These studies provided tremendous advances in the way we understand organisms, and because of those advances, this is an optimal time to begin to think about how those parts interact within organisms. The work presented here offers a new way to analyze and interpret behaviors that can lead to novel insights into how an organism functions. By providing new hypotheses and methods to assess integration as a measure of organismal performance, the tools are now readily available for other researchers to apply these ideas to their own work.

Integration is an emergent property of functional systems that is not apparent unless the interactions between traits are examined, and in this way integration provides a novel mechanism for understanding how organisms work. For example, if traits related to feeding ability were considered in isolation, the two species of sculpin analyzed above would be considered functionally similar, although there are potentially large differences in performance between them when traits are considered simultaneously. We have demonstrated the importance of specialization in

constraining strategies, and suggest that because of this, integration may be an important factor regulating the evolution of locomotor and feeding systems—changes in one system can limit the changes available to the other system. Additionally, we demonstrate that variation within and between species can be complex, involving differences in the magnitude and composition of integration, and also the number of axes that define integration. This variation suggests that differences in integration may actually be a trait upon which selection can act, again influencing the evolution of performance. Finally, we demonstrate the importance of two variables, speed of swimming and size of mouth, in defining integration between and among species. If this result proves to be ubiquitous across fishes in future work, it would suggest that, despite the large number of functional components and high diversity in fishes, most might be subject to a similar primary constraint. This idea represents a significant advance in our goal of understanding organisms via simple patterns and rules. Together, these insights should stimulate future work to consider the ability of traits to influence each other, and we hope that those that continue to study feeding in fishes can have a deeper appreciation for the role of locomotion in driving those patterns. To parody Dobzhansky (1973), “Nothing in fish feeding makes sense except in the light of integration”.

The novel approach to organismal performance taken throughout this review has demonstrated important concepts that have not been considered previously and stimulates further thought into factors contributing to a species' ability to survive in its environment. These analyses are only a first step, and many more questions can be asked regarding the ecological and evolutionary significance of integration. Additionally, it is important to recognize that although this current work focuses on specific kinematic-traits in fishes, similar patterns and relationships might also be important across additional performance-systems (i.e., sensory systems) and taxa. From these perspectives, several future questions on the relevance of integration for organisms emerge. For example, how repeatable (stereotyped) or flexible is integration (Wainwright et al. 2008)? Is variation in integration ecologically relevant (Bolnick et al. 2003)? What is the role of integration in adaptation (Ghalambor et al. 2003, 2004)? Does it constrain organisms from adapting to new environments because strong integration is difficult to break apart (Pigliucci 2003; Hansen and Houle 2004)? Or does it facilitate adaptation because tight links facilitate rapid evolutionary feedback and punctuated changes (Eldredge

and Gould 1972; Seaborg 1999)? How does performance-integration regulate evolution of locomotor and feeding modes? Are some modes more difficult to evolve than others? These questions can potentially direct future study of integrated kinematic-traits, and fishes may continue to provide a model taxon for study within which to address these questions. Complexity, integration, and emergence are becoming more prominent ideas in organismal biology, and may represent a new frontier in biological research that can both inform and be informed by the mechanics and diversity of feeding in fishes.

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Supplementary data

Supplementary Data available at *ICB* online.

References

- Abdi H. 2010. Partial least squares regression and projection on latent structure regression (PLS Regression). *Wiley Interdiscip Rev Comput Stat* 2:97–106.
- Adams DC, Felice RN. 2014. Assessing trait covariation and morphological integration on phylogenies using evolutionary covariance matrices. *PLoS One* 9:e94335.
- Alexander RM. 1991. Optimum timing of muscle activation for simple models of throwing. *J Theor Biol* 150:349–72.
- Alexander RM. 2003. *Principles of animal locomotion*. Princeton (NJ): Princeton University Press.
- Altenbach JS. 1989. Prey capture by the fishing bats *Noctilio leporinus* and *Myotis vivesi*. *J Mamm* 70:421–4.
- Anderson CW. 1993. The modulation of feeding behavior in response to prey types in the frog *Rana pipiens*. *J Exp Biol* 179:1–12.
- Arnold SJ. 1983. Morphology, performance and fitness. *Am Zool* 23:347–61.

- Badyaev AV, Foresman KR, Young RL. 2005. Evolution of morphological integration: Developmental accommodation of stress-induced variation. *Am Nat* 166:382–95.
- Bak P. 1996. *How nature works*. New York (NY): Springer-Verlag.
- Bak P, Tang C, Wiesenfeld K. 1988. Self-organized criticality. *Phys Rev A* 38:364–74.
- Bastir M, Rosas A. 2005. Hierarchical nature of morphological integration and modularity in the human posterior face. *Am J Phys Anthropol* 128:26–34.
- Bates KT, Falkingham PL. 2012. Estimating maximum bite performance in *Tyrannosaurus rex* using multi-body dynamics. *Biol Lett* 8:660–4.
- Bayliss WM. 1921. Integration in the living organism. *Nature* 108:537–9.
- Bels VL, Davenport J, Delheusy V. 1997. Kinematic analysis of the feeding behavior in the box turtle *Terrapene carolina* (L.), (Reptilia: Emydidae). *J Exp Zool* 277:198–212.
- Berg RL. 1960. The ecological significance of correlation pleiades. *Evolution* 14:171–80.
- Bergert BA, Wainwright PC. 1997. Morphology and kinematics of prey capture in the syngnathid fishes *Hippocampus erectus* and *Syngnathus floridae*. *Mar Biol* 127:563–70.
- Biewener AA. 2003. *Animal locomotion*. New York (NY): Oxford University Press.
- Bimbard GI, Kolomenskiy D, Bouteleux O, Casas JRM, Godoy-Diana R. 2013. Force balance in the take-off of a pierid butterfly: relative importance and timing of leg impulsion and aerodynamic forces. *J Exp Biol* 216:3551–63.
- Bishop KL, Wainwright PC, Holzman R. 2008. Anterior-to-posterior wave of buccal expansion in suction feeding fishes is critical for optimizing fluid flow velocity profile. *J R Soc Interface* 5:1309–16.
- Blake RW. 2004. Fish functional design and swimming performance. *J Fish Biol* 65:1193–222.
- Blake RW. 2006. Biomechanics of rheotaxis in six teleost genera. *Can J Zool* 84:1173–86.
- Bolnick D, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulseley CD, Forister ML. 2003. The ecology of individuals: Incidence and implications of individual specialization. *Am Nat* 161:1–28.
- Bookstein FL, Gunz P, Mitteroecker P, Prossinger H, Schaefer K, Seidler H. 2003. Cranial integration in *Homo*: Singular warps analysis of the midsagittal plane in ontogeny and evolution. *J Hum Evol* 44:167–87.
- Boulesteix A-L, Strimmer K. 2007. Partial least squares: A versatile tool for the analysis of high-dimensional genomic data. *Brief Bioinform* 8:32–44.
- Cáceres N, Meloro C, Carotenuto F, Passaro F, Sponchiado J, Melo GL, Raia P. 2014. Ecogeographical variation in skull shape of capuchin monkeys. *J Biogeogr* 41:501–12.
- Camazine S. 2003. *Self-organization in biological systems*. Princeton (NJ): Princeton University Press.
- Camp A, Brainerd E. 2014. Role of axial muscles in powering mouth expansion during suction feeding in largemouth bass. *J Exp Biol* 217:1333–45.
- Carrascal LM, Galvan I, Gordo O. 2009. Partial least squares regression as an alternative to current regression methods used in ecology. *Oikos* 118:681–90.
- Carroll AM, Wainwright PC, Huskey SH, Collar DC, Turingan RG. 2004b. Morphology predicts suction feeding performance in centrarchid fishes. *J Exp Biol* 207:3873–81.
- Cheverud JM. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution* 36:499–516.
- Collar DC, Near TJ, Wainwright PC. 2005. Comparative analysis of morphological diversity: Does disparity accumulate at the same rate in two lineages of centrarchid fishes? *Evolution* 59:1783–94.
- Collar DC, Wainwright PC, Alfaro ME. 2008. Integrated diversification of locomotion and feeding in labrid fishes. *Biol Lett* 4:84–6.
- Collar DC, Wainwright PC, Alfaro ME, Revell LJ, Mehta RS. 2014. Biting disrupts integration to spur skull evolution in eels. *Nat Commun* 5:5505.
- Combes SA, Crall JD, Mukherjee S. 2010. Dynamics of animal movement in an ecological context: Dragonfly wing damage reduces flight performance and predation success. *Biol Lett* 6:426–9.
- Copus JM, Gibb AC. 2013. A forceful upper jaw facilitates picking-based prey capture: Biomechanics of feeding in a butterflyfish, *Chaetodon trichrous*. *Zoology* 116:336–47.
- Coughlin DJ. 1991. Ontogeny of feeding behavior of first-feeding Atlantic salmon (*Salmo salar*). *Can J Fish Aquat Sci* 48:1896–904.
- Darwin C. 1859. *On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life*. London: Murray.
- Darwin C. 1868. *The variation of animals and plants under domestication*. London: Murray.
- Day SW, Higham TE, Cheer AY, Wainwright PC. 2005. Spatial and temporal patterns of water flow generated by suction-feeding bluegill sunfish *Lepomis macrochirus* resolved by Particle Image Velocimetry. *J Exp Biol* 208:2661–71.
- Day SW, Higham TE, Wainwright PC. 2007. Time resolved measurements of the flow generated by suction feeding fish. *Exp Fluids* 43:713–24.
- de Haan J. 2006. How emergence arises. *Ecol Complex* 3:293–301.
- de Jong S. 1993. SIMPLS: An alternative approach to partial least squares regression. *Chemometr Intell Lab Syst* 18:251–63.
- Dean MN, Bizarro JJ, Summers AP. 2007. The evolution of cranial design, diet, and feeding mechanisms in batoid fishes. *Integr Comp Biol* 47:70–81.
- Deban SM, O'Reilly JC, Dicke U, van Leeuwen JL. 2007. Extremely high-power tongue projection in plethodontid salamanders. *J Exp Biol* 210:655–67.
- Dobzhansky T. 1973. Nothing in biology makes sense except in the light of evolution. *Am Biol Teach* 35:125–9.
- Domenici P, Blake RW. 1997. The kinematics and performance of fish fast-start swimming. *J Exp Biol* 200:1165–78.
- Domenici P, Turesson H, Brdensen J, Brönmark C. 2008. Predator-induced morphology enhances escape locomotion in crucian carp. *Proc R Soc B Biol Sci* 275:195–201.
- Drucker E, Jensen J. 1996. Pectoral fin locomotion in the striped surfperch. II. Scaling swimming kinematics and performance at a gait transition. *J Exp Biol* 199:2243–52.

- Drucker EG, Lauder GV. 1999. Locomotor forces on a swimming fish: Three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. *J Exp Biol* 202:2393–412.
- Dullemeijer P. 1974. Concepts and approaches in animal morphology. Assen, The Netherlands: Van Gorcum & Comp. BV.
- Eldredge N, Gould SJ. 1972. Punctuated equilibria: An alternative to phyletic gradualism. In: Schopf TJM, editor. Models in paleobiology. San Francisco (CA): Freeman, Cooper, and Company. p. 82–115.
- Falk B, Jakobsen L, Surlykke A, Moss CF. 2014. Bats coordinate sonar and flight behavior as they forage in open and cluttered environments. *J Exp Biol* 217:4356–64.
- Ferry-Graham LA, Gibb AC, Hernandez LP. 2008. Premaxillary movements in cyprinodontiform fishes: An unusual protrusion mechanism facilitates “picking” prey capture. *Zoology* 111:455–66.
- Ferry-Graham LA, Wainwright PC, Westneat MW, Bellwood DR. 2001. Modulation of prey capture kinematics in the cheeklined wrasse *Oxycheilinus digrammus* (Teleostei: labridae). *J Exp Zool* 290:88–100.
- Ferry-Graham LA, Wainwright PC, Westneat MW, Bellwood DR. 2002. Mechanisms of benthic prey capture in wrasses (Labridae). *Mar Biol* 141:819–30.
- Foster KL, Higham TE. 2014. Context-dependent changes in motor control and kinematics during locomotion: Modulation and decoupling. *Proc R Soc B Biol Sci* 281:20133331.
- Frazetta TH. 1975. Complex adaptations in evolving populations. Sunderland (MA): Sinauer Associates.
- Frazetta TH, Prange CD. 1987. Movements of cephalic components during feeding in some requiem sharks (Carcharhiniformes, Carcharhinidae). *Copeia* 1987:979–93.
- Froese R, Pauly D. 2014. 2014. Fishbase [Internet]. Version 04/2014 (<http://www.fishbase.org>).
- Fulton CF, Bellwood DB, Wainwright PW. 2001. The relationship between swimming ability and habitat use in wrasses (Labridae). *Mar Biol* 139:25–33.
- Gardiner JM, Motta PJ. 2012. Largemouth bass (*Micropterus salmoides*) switch feeding modalities in response to sensory deprivation. *Zoology* 115:78–83.
- Garland T Jr. 1994. Quantitative genetics of locomotor behavior and physiology in a garter snake. In: Boake CRB, editor. Quantitative genetic studies of behavioral evolution. Chicago (IL): The University of Chicago Press. p. 251–77.
- Garland T Jr, Losos JB. 1994. Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright PC, Reilly SM, editors. Ecological morphology: integrative organismal biology. Chicago (IL): University of Chicago Press. p. 240–302.
- Garthwaite PH. 1994. An interpretation of partial least squares. *J Am Stat Assoc* 89:122–7.
- Gething M-J, Sambrook J. 1992. Protein folding in the cell. *Nature* 355:33–45.
- Ghalambor CK, Reznick DN, Walker JA. 2004. Constraints on adaptive evolution: The functional trade-off between reproduction and fast-start swimming performance in the Trinidadian guppy (*Poecilia reticulata*). *Am Nat* 164:38–50.
- Ghalambor CK, Walker JA, Reznick DN. 2003. Multi-trait selection, adaptation, and constraints on the evolution of burst swimming performance. *Integr Comp Biol* 43:431–8.
- Gibb A, Ferry-Graham L, Hernandez LP, Romansco R, Blanton J. 2008. Functional significance of intramandibular bending in Poeciliid fishes. *Environ Biol Fish* 83:507–19.
- Gould SJ. 2002. The structure of evolutionary theory. Cambridge (MA): The Belknap Press.
- Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proc R Soc B Biol Sci* 285:581–98.
- Haenlein M, Kaplan AM. 2004. A beginner’s guide to partial least squares analysis. *Understand Stat* 3:283–97.
- Hansen TF, Houle D. 2004. Evolvability, stabilizing selection, and the problem of stasis. In: Pigliucci M, Preston K, editors. Phenotypic integration: Studying the ecology and evolution of complex phenotypes. New York (NY): Oxford University Press. p. 130–50.
- Harper DG, Blake RW. 1991. Prey capture and the fast-start performance of Northern pike *Esox lucius*. *J Exp Biol* 155:175–92.
- Harris JE. 1936. The role of the fins in the equilibrium of the swimming fish: I. Wind-tunnel tests on a model of *Mustelus canis* (Mitchill). *J Exp Biol* 13:476–93.
- Herrel A, Bonneaud C. 2012. Trade-offs between burst performance and maximal exertion capacity in a wild amphibian, *Xenopus tropicalis*. *J Exp Biol* 215:3106–11.
- Herrel A, O’Reilly JC, Richmond AM. 2002. Evolution of bite performance in turtles. *J Evol Biol* 15:1083–94.
- Herrel A, Podos J, Huber SK, Hendry AP. 2005. Evolution of bite force in Darwin’s finches: A key role for head width. *J Evol Biol* 18:669–75.
- Higham TE. 2007a. Feeding, fins and braking maneuvers: Locomotion during prey capture in centrarchid fishes. *J Exp Biol* 210:107–17.
- Higham TE. 2007b. The integration of locomotion and prey capture in vertebrates: Morphology, behavior, and performance. *Integr Comp Biol* 47:82–95.
- Higham TE, Day SW, Wainwright PC. 2005. Sucking while swimming: Evaluating the effects of ram speed on suction generation in bluegill sunfish *Lepomis macrochirus* using digital particle image velocimetry. *J Exp Biol* 208:2653–60.
- Higham TE, Day SW, Wainwright PC. 2006a. Multidimensional analysis of suction feeding performance in fishes: Fluid speed, acceleration, strike accuracy and the ingested volume of water. *J Exp Biol* 209:2713–25.
- Higham TE, Day SW, Wainwright PC. 2006b. The pressures of suction feeding: The relation between buccal pressure and induced fluid speed in centrarchid fishes. *J Exp Biol* 209:3281–7.
- Higham TE, Hulsey CD, Rican O, Carroll AM. 2007. Feeding with speed: Prey capture evolution in cichlids. *J Evol Biol* 20:70–8.
- Holter NS, Mitra M, Maritan A, Cieplak M, Banavar JR, Fedoroff NV. 2000. Fundamental patterns underlying gene expression profiles: Simplicity from complexity. *Proc Natl Acad Sci USA* 97:8409–14.
- Holzman R, Collar DC, Day SW, Bishop KL, Wainwright PC. 2008a. Scaling of suction-induced flows in bluegill: Morphological and kinematic predictors for the ontogeny of feeding performance. *J Exp Biol* 211:2658–68.

- Holzman R, Collar DC, Mehta RS, Wainwright PC. 2012. An integrative modeling approach to elucidate suction-feeding performance. *J Exp Biol* 215:1–13.
- Holzman R, Day SW, Mehta RS, Wainwright PC. 2008b. Integrating the determinants of suction feeding performance in centrarchid fishes. *J Exp Biol* 211:3296–305.
- Holzman R, Day SW, Wainwright PC. 2007. Timing is everything: Coordination of strike kinematics affects the force exerted by suction feeding fish on attached prey. *J Exp Biol* 210:3328–36.
- Huber DR, Eason TG, Hueter RE, Motta PJ. 2005. Analysis of bite force and mechanical design of the feeding mechanism of the durophagous horn shark *Heterodontus francisci*. *J Exp Biol* 208:3553–71.
- Husak JF. 2006. Does speed help you survive? A test with Collared Lizards of different ages. *Funct Ecol* 20:174–9.
- Irschick DJ, Meyers JJ, Husak JF, Le Galliard J. 2008. How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evol Ecol Res* 10:177–96.
- Jagnandan K, Sanford CP. 2013. Kinematics of ribbon-fin locomotion in the bowfin, *Amia calva*. *J Exp Zool Part A Ecol Genet Physiol* 319:569–83.
- Jayne BC, Bennett AF. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* 44:1204–29.
- Johansson RS, Cole KJ. 1992. Sensory-motor coordination during grasping and manipulative actions. *Curr Opin Neurobiol* 2:815–23.
- Kane EA. 2014. Integration of functional systems: Assessing the use of the locomotor system during prey capture in fishes [PhD Dissertation]. [Riverside, CA]: University of California, Riverside.
- Kane EA, Higham TE. 2011. The integration of locomotion and prey capture in divergent cottid fishes: Functional disparity despite morphological similarity. *J Exp Biol* 214:1092–9.
- Kane EA, Higham TE. 2012. Life in the flow lane: Differences in pectoral fin morphology suggest transitions in station-holding demand across species of marine sculpin. *Zoology* 115:223–32.
- Kane EA, Higham TE. 2014. Modelled three-dimensional suction accuracy predicts prey capture success in three species of centrarchid fishes. *J R Soc Interface* 11:20140223.
- Karim FD, Thummel CS. 1992. Temporal coordination of regulatory gene expression by the steroid hormone ecdysone. *EMBO J* 11:4083–93.
- Klingenberg CP. 2008. Morphological integration and developmental modularity. *Annu Rev Ecol Evol Syst* 39:115–32.
- Klingenberg CP, Duttke S, Whelan S, Kim M. 2011. Developmental plasticity, morphological variation and evolvability: A multilevel analysis of morphometric integration in the shape of compound leaves. *J Evol Biol* 25:115–29.
- Klingenberg CP, Zaklan SD. 2000. Morphological integration between developmental compartments in the *Drosophila* wing. *Evolution* 54:1273–85.
- Korn RW. 2005. The emergence principle in biological hierarchies. *Biol Phil* 20:137–51.
- Korsmeyer KE, Steffensen JF, Herskin J. 2002. Energetics of median and paired fin swimming, body and caudal fin swimming, and gait transition in parrotfish (*Scarus schlegelii*) and triggerfish (*Rhinecanthus aculeatus*). *J Exp Biol* 205:1253–63.
- Krishnan A, Williams LJ, McIntosh AR, Abdi H. 2011. Partial least squares (PLS) methods for neuroimaging: A tutorial and review. *NeuroImage* 56:455–75.
- Langerhans RB. 2009. Morphology, performance, fitness: Functional insight into a post-Pleistocene radiation of mosquitofish. *Biol Lett* 5:488–91.
- Lauder GV. 1982. Patterns of evolution in the feeding mechanism of actinopterygian fishes. *Am Zool* 22:275–85.
- Lauder GV. 1985. Aquatic feeding in lower vertebrates. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, editors. *Functional vertebrate morphology*. Cambridge (MA): Harvard University Press. p. 210–29.
- Lauder GV. 2000a. Biomechanics and behavior: Analyzing the mechanistic basis of movement from an evolutionary perspective. In: Domenici P, Blake RW, editors. *Biomechanics in animal behavior*. Oxford: BIOS scientific Publishers, Ltd. p. 19–32.
- Lauder GV. 2000b. Function of the caudal fin during locomotion in fishes: Kinematics, flow visualization, and evolutionary patterns. *Am Zool* 40:101–22.
- Lauder GV, Liem KF. 1981. Prey capture by *Luciocephalus pulcher*: Implications for models of jaw protrusion in teleost fishes. *Environ Biol Fish* 6:257–68.
- Lauder GV, Tytell ED. 2005. Hydrodynamics of undulatory propulsion. In: Robert ES, George VL, editors. *Fish physiology: Fish biomechanics*. San Diego (CA): Academic Press. p. 425–68.
- Law T, Blake R. 1996. Comparison of the fast-start performances of closely related, morphologically distinct threespine sticklebacks (*Gasterosteus* spp.). *J Exp Biol* 199:2595–604.
- Lemell P, Weisgram J. 1996. Feeding patterns of *Pelusios castaneus* (Chelonian: Pleurodira). *Neth J Zool* 47:429–41.
- Levit GS, Hossfeld U, Olsson L. 2004. The integration of darwinism and evolutionary morphology: Alexej Nikolajevich Sewertzoff (1866–1936) and the developmental basis of evolutionary change. *J Exp Zool (Mol Dev Evol)* 302B:343–54.
- Liem KF. 1978. Modulatory multiplicity in functional repertoire of feeding mechanism in cichlid fishes: 1. Piscivores. *J Morphol* 158:323–60.
- Liem KF, Summers AP. 2000. Integration of versatile functional design, population ecology, ontogeny and phylogeny. *Neth J Zool* 50:245–59.
- Long J, Mchenry M, Boetticher N. 1994. Undulatory swimming: How traveling waves are produced and modulated in sunfish (*Lepomis gibbosus*). *J Exp Biol* 192:129–45.
- Lönstedt OM, McCormick MI, Meekan MG, Ferrari MCO, Chivers DP. 2012. Learn and live: Predator experience and feeding history determines prey behaviour and survival. *Proc R Soc B Biol Sci* 279:2091–8.
- Losos JB, Sinervo B. 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J Exp Biol* 145:23–30.
- Marshall CD, Guzman A, Narazaki T, Sato K, Kane EA, Sterba-Boatwright BD. 2012. The ontogenetic scaling of bite force and head size in loggerhead sea turtles (*Caretta caretta*): Implications for durophagy in neritic, benthic habitats. *J Exp Biol* 215:4166–74.

- Marugán-Lobón J, Buscalioni ÁD. 2006. Avian skull morphological evolution: Exploring exo- and endocranial covariation with two-block partial least squares. *Zoology* 109:217–30.
- Matott MP, Motta PJ, Hueter RE. 2005. Modulation in feeding kinematics and motor pattern of the nurse shark *Ginglymostoma cirratum*. *Environ Biol Fish* 74:163–74.
- McBrayer LD. 2004. The relationship between skull morphology, biting performance and foraging mode in Kalahari lacertid lizards. *Zool J Linn Soc* 140:403–16.
- McElroy EJ, Hickey KL, Reilly SM. 2008. The correlated evolution of biomechanics, gait and foraging mode in lizards. *J Exp Biol* 211:1029–40.
- McElroy EJ, Reilly SM. 2009. The relationship between limb morphology, kinematics, and force during running: The evolution of locomotor dynamics in lizards. *Biol J Linn Soc* 97:634–51.
- McGuire JL. 2010. Geometric morphometrics of vole (*Microtus californicus*) dentition as a new paleoclimate proxy: Shape change along geographic and climatic clines. *Quat Int* 212:198–205.
- Mehta RS, Wainwright PC. 2007. Biting releases constraints on moray eel feeding kinematics. *J Exp Biol* 210:495–504.
- Merilä J, Björklund M. 2004. Phenotypic integration as a constraint and adaptation. In: Pigliucci M, Preston K, editors. *Phenotypic integration: Studying the ecology and evolution of complex phenotypes*. New York (NY): Oxford University Press. p. 107–29.
- Mevik B, Wehrens R. 2007. The pls package: Principal component and partial least squares regression in R. *J Stat Softw* 18:1–24.
- Miles DB, Sinervo B, Frankino WA. 2000. Reproductive burden, locomotor performance, and the cost of reproduction in free ranging lizards. *Evolution* 54:1386–95.
- Mitteroecker P, Bookstein F. 2008. The evolutionary role of modularity and integration in the hominoid cranium. *Evolution* 62:943–58.
- Montuelle SJ, Herrel A, Libourel P-A, Daillie S, Bels VL. 2012a. Flexibility in locomotor and feeding integration during prey capture in varanid lizards: Effects of prey size and velocity. *J Exp Biol* 215:3823–35.
- Montuelle SJ, Herrel A, Libourel P-A, Daillie S, Bels VL. 2012b. Prey capture in lizards: Differences in jaw-neck-forelimb coordination. *Biol J Linn Soc* 105:607–22.
- Montuelle SJ, Herrel A, Libourel PA, Reveret L, Bels VL. 2009. Locomotor-feeding coupling during prey capture in a lizard (*Gerrhosaurus major*): Effects of prehension mode. *J Exp Biol* 212:768–77.
- Motta PJ. 1984. Mechanics and functions of jaw protrusion in teleost fishes—a review. *Copeia* 1984:1–18.
- Motta PJ, Hueter RE, Tricas TC, Summers AP. 2002. Kinematic analysis of suction feeding in the nurse shark, *Ginglymostoma cirratum* (Orectolobiformes, Ginglymostomatidae). *Copeia* 2002:24–38.
- Muller M, Osse JWM. 1984. Hydrodynamics of suction feeding in fish. *Trans Zool Soc Lond* 37:51–135.
- Muller M, Osse JWM, Verhagen JHG. 1982. A quantitative hydrodynamic model of suction feeding in fish. *J Theor Biol* 95:49–79.
- Nathan R. 2008. An emerging movement ecology paradigm. *Proc Natl Acad Sci USA* 105:19050–1.
- Nekaris KAI, Rasmussen DT. 2003. Diet and feeding behavior of Mysore slender lorises. *Int J Primatol* 24:33–46.
- Nemeth DH. 1997. Modulation of attack behavior and its effect on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. *J Exp Biol* 200:2155–64.
- Norton SF, Brainerd EL. 1993. Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J Exp Biol* 176:11–29.
- Nyberg DW. 1971. Prey capture in the largemouth bass. *Am Midland Nat* 86:128–44.
- Olson EC, Miller RL. 1951. A mathematical model applied to a study of the evolution of species. *Evolution* 5:325–38.
- Olson EC, Miller RL. 1958. *Morphological integration*. Chicago (IL): The University of Chicago Press.
- Onuchic JN, Wolynes PG. 2004. Theory of protein folding. *Curr Opin Struct Biol* 14:70–5.
- Oufiero CE, Holzman RA, Young FA, Wainwright PC. 2012. New insights from serranid fishes on the role of trade-offs in suction-feeding diversification. *J Exp Biol* 215:3845–55.
- Oufiero CE, Walsh MR, Reznick DN, Garland T. 2011. Swimming performance trade-offs across a gradient in community composition in Trinidadian killifish (*Rivulus hartii*). *Ecology* 92:170–9.
- Peres-Neto P, Magnan P. 2004. The influence of swimming demand on phenotypic plasticity and morphological integration: A comparison of two polymorphic charr species. *Oecologia* 140:36–45.
- Pigliucci M. 2003. Phenotypic integration: Studying the ecology and evolution of complex phenotypes. *Ecol Lett* 6:265–72.
- Porges SW. 1998. Love: An emergent property of the mammalian autonomic nervous system. *Psychoneuroendocrinology* 23:837–61.
- Porto A, de Oliveira F, Shirai L, De Conto V, Marroig G. 2009. The evolution of modularity in the mammalian skull I: Morphological integration patterns and magnitudes. *BMC Evol Biol* 36:118–35.
- Qureshi I, Compeau D. 2009. Assessing between-group differences in information systems research: A comparison of covariance- and component-based SEM. *MIS Quart* 33:197–214.
- Rand DM, Lauder GV. 1981. Prey capture in the chain pickerel, *Esox niger*: Correlations between feeding and locomotor behavior. *Can J Zool* 59:1072–8.
- Reid AL, Seebacher F, Ward AJW. 2010. Learning to hunt: The role of experience in predator success. *Behaviour* 147:223–33.
- Reynolds CW. 1987. Flocks, herds and schools: A distributed behavioral model. *Comput Graph* 21:25–34.
- Rice AN. 2008. Coordinated mechanics of feeding, swimming, and eye movements in *Tautoga onitis*, and implications for the evolution of trophic strategies in fishes. *Mar Biol* 154:255–67.
- Rice AN, Cooper WJ, Westneat MW. 2008. Diversification of coordination patterns during feeding behaviour in cheiline wrasses. *Biol J Linn Soc* 93:289–308.
- Rice AN, Westneat MW. 2005. Coordination of feeding, locomotor and visual systems in parrotfishes (Teleostei: Labridae). *J Exp Biol* 208:3503–18.
- Rohlf FJ, Corti M. 2000. Use of two-block partial least-squares to study covariation in shape. *Syst Biol* 49:740–53.

- Roos G, Leysen H, Van Wassenbergh S, Herrel A, Jacobs P, Dierick M, Aerts P, Adriaens D. 2009. Linking morphology and motion: A test of a four-bar mechanism in seahorses. *Physiol Biochem Zool* 82:7–19.
- Roseman CC, Weaver TD, Stringer CB. 2011. Do modern humans and Neandertals have different patterns of cranial integration? *J Hum Evol* 60:684–93.
- Rosen RA, Hales DC. 1981. Feeding of paddlefish, *Polyodon spathula*. *Copeia* 1981:441–55.
- Rupp MF, Hulsey CD. 2014. Influence of substrate orientation on feeding kinematics and performance of algae-grazing Lake Malawi cichlid fishes. *J Exp Biol* 217:3057–66.
- Sanford CPJ, Wainwright PC. 2002. Use of sonomicrometry demonstrates the link between prey capture kinematics and suction pressure in largemouth bass. *J Exp Biol* 205:3445–57.
- Seaborg DM. 1999. Evolutionary feedback: A new mechanism for stasis and punctuated evolutionary change based on integration of the organism. *J Theor Biol* 198:1–26.
- Seigel RA, Huggins MM, Ford NB. 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia* 73:481–5.
- Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: An ecological and evolutionary overview. *Trends Ecol Evol* 19:372–8.
- Skorczewski T, Cheer A, Wainwright PC. 2012. The benefits of planar circular mouths on suction feeding performance. *J R Soc Interface* 9:1767–73.
- Solé RV, Goodwin B. 2000. Signs of life: How complexity pervades biology. New York (NY): Basic Books.
- Solé RV, Manrubia SC, Benton M, Kauffman S, Bak P. 1999. Criticality and scaling in evolutionary ecology. *Trends Ecol Evol* 14:156–60.
- Sterck EHM, Begeer S. 2010. Theory of Mind: Specialized capacity or emergent property? *Eur J Dev Psychol* 7:1–16.
- Taft NK, Lauder GV, Madden PGA. 2008. Functional regionalization of the pectoral fin of the benthic longhorn sculpin during station holding and swimming. *J Zool* 276:159–67.
- Tomita T, Sato K, Suda K, Kawachi J, Nakaya K. 2011. Feeding of the megamouth shark (Pisces: Lamniformes: Megachasmidae) predicted by its hyoid arch: A biomechanical approach. *J Morphol* 272:513–524.
- Tran HQ, Mehta RS, Wainwright PC. 2010. Effects of ram speed on prey capture kinematics of juvenile Indo-Pacific tarpon, *Megalops cyprinoides*. *Zoology* 113:75–84.
- Tricas TC, McCosker JE. 1984. Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. *Proc Calif Acad Sci* 43:221–38.
- Tytell ED, Lauder GV. 2008. Hydrodynamics of the escape response in bluegill sunfish, *Lepomis macrochirus*. *J Exp Biol* 211:3359–69.
- Van Leeuwen JL. 1984. A quantitative study of flow in prey capture by rainbow trout, *Salmo gairdneri* with general consideration of the actinopterygian feeding mechanism. *Trans Zool Soc Lond* 37:171–227.
- Van Wassenbergh S, Aerts P, Adriaens D, Herrel A. 2005. A dynamic model of mouth closing movements in clariid catfishes: The role of enlarged jaw adductors. *J Theor Biol* 234:49–65.
- Van Wassenbergh S, De Rechter D. 2011. Piscivorous cyprinid fish modulates suction feeding kinematics to capture elusive prey. *Zoology* 114:46–52.
- Van Wassenbergh S, Herrel A, Adriaens D, Aerts P. 2006. Modulation and variability of prey capture kinematics in clariid catfishes. *J Exp Zool A* 305A:559–69.
- Van Wassenbergh S, Herrel A, Adriaens D, Aerts P. 2007b. No trade-off between biting and suction feeding performance in clariid catfishes. *J Exp Biol* 210:27–36.
- Van Wassenbergh S, Roos G, Genbrugge A, Leysen H, Aerts P, Adriaens D, Herrel A. 2009. Suction is kid's play: Extremely fast suction in newborn seahorses. *Biol Lett* 5:200–3.
- Vicario DS. 2004. Using learned calls to study sensory-motor integration in songbirds. *Ann NY Acad Sci* 1016:246–62.
- Viscido SV, Parrish JK, Grünbaum D. 2004. Individual behavior and emergent properties of fish schools: A comparison of observation and theory. *Mar Ecol Prog Ser* 273:271–2.
- Vitousek PM. 1990. Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. *Oikos* 57:7–13.
- Wainwright PC. 1996. Ecological explanation through functional morphology: The feeding biology of sunfishes. *Ecology* 77:1336–43.
- Wainwright PC, Bellwood DR, Westneat MW. 2002. Ecomorphology of locomotion in labrid fishes. *Environ Biol Fish* 65:47–62.
- Wainwright PC, Carroll AM, Collar DC, Day SW, Higham TE, Holzman RA. 2007. Suction feeding mechanics, performance, and diversity in fishes. *Integr Comp Biol* 47:96–106.
- Wainwright PC, Ferry-Graham LA, Waltzek TB, Carroll AM, Hulsey CD, Grubich JR. 2001. Evaluating the use of ram and suction during prey capture by cichlid fishes. *J Exp Biol* 204:3039–51.
- Wainwright PC, Lauder GV. 1986. Feeding biology of sunfishes: Patterns of variation in the feeding mechanism. *Zool J Linn Soc* 88:217–28.
- Wainwright PC, Mehta RS, Higham TE. 2008. Stereotypy, flexibility and coordination: Key concepts in behavioral functional morphology. *J Exp Biol* 211:3523–8.
- Wainwright PC, Shaw SS. 1999. Morphological basis of kinematic diversity in feeding sunfishes. *J Exp Biol* 202:3101–10.
- Wake DB, Roth G. 1989. Complex organismal functions: Integration and evolution in vertebrates. New York (NY): John Wiley & Sons.
- Wakeling JM, Johnston IA. 1998. Muscle power output limits fast-start performance in fish. *J Exp Biol* 201:1505–26.
- Walker JA. 2004. Kinematics and performance of maneuvering control surfaces in teleost fishes. *IEEE J Ocean Eng* 29:572–84.
- Walker JA. 2007. A general model of functional constraints on phenotypic evolution. *Am Nat* 170:681–9.
- Walker JA. 2010. An integrative model of evolutionary covariance: A symposium on body shape in fishes. *Integr Comp Biol* 50:1051–6.

- Walker JA, Ghalambor CK, Griset OL, McKenney D, Reznick DN. 2005. Do faster starts increase the probability of evading predators? *Funct Ecol* 19:808–15.
- Walker JA, Westneat MW. 2002a. Kinematics, dynamics, and energetics of rowing and flapping propulsion in fishes. *Integr Comp Biol* 42:1032–43.
- Walker JA, Westneat MW. 2002b. Performance limits of labri-form propulsion and correlates with fin shape and motion. *J Exp Biol* 205:177–87.
- Webb PW. 1978. Fast-start performance and body form in seven species of teleost fish. *J Exp Biol* 74:211–26.
- Webb PW. 1982a. Avoidance responses of fathead minnow to strikes by four teleost predators. *J Comp Physiol* 147:371–8.
- Webb PW. 1982b. Locomotor patterns in the evolution of Actinopterygian fishes. *Am Zool* 22:329–42.
- Webb PW. 1984a. Body and fin form and strike tactics of four teleost predators attacking fathead minnow (*Pimephales promelas*) prey. *Can J Fish Aquat Sci* 41:157–65.
- Webb PW. 1984b. Body form, locomotion, and foraging in aquatic vertebrates. *Am Zool* 24:107–20.
- Webb PW, Gerstner CL, Minton ST. 1996. Station-holding by the mottled sculpin, *Cottus bairdi* (Teleostei: Cottidae), and other fishes. *Copeia* 1996:488–93.
- Webb PW, Skadsen JM. 1980. Strike tactics of *Esox*. *Can J Zool* 58:1462–9.
- Westneat MW, Wainwright PC, Bellwood DR. 1999. Diversity of mechanical design for feeding in labrid fishes. *Am Zool* 39:591.
- Wintzer AP, Motta PJ. 2005. A comparison of prey capture kinematics in hatchery and wild *Micropterus salmoides floridanus*: Effects of ontogeny and experience. *J Fish Biol* 67:409–27.
- Wold H. 1975. Soft modelling by latent variables; the nonlinear iterative partial least squares approach. In: Gani J, editor. *Perspectives in probability and statistics. Papers in honour of M. S. Barlett*. London: Academic Press. p. 117–42.
- Wold S, Sjöström M, Eriksson L. 2001. PLS-regression: A basic tool of chemometrics. *Chemometr Intell Lab Syst* 58:109–30.
- Zelditch ML, Bookstein FL, Lundrigan BL. 1992. Ontogeny of integrated skull growth in the cotton rat *Sigmodon fulviventer*. *Evolution* 46:1164–80.
- Zelditch ML, Mezey J, Sheets HD, Lundrigan BL, Garland T Jr. 2006. Developmental regulation of skull morphology II: Ontogenetic dynamics of covariance. *Evol Dev* 8:46–60.
- Zelditch ML, Swiderski DL, Sheets HD, Fink WL. 2004. *Geometric morphometrics for biologists: A primer*. San Diego (CA): Elsevier Academic Press.
- Zweers GA. 1979. Explanation of structure by optimization and systematization. *Neth J Zool* 29:418–40.