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Beyond Suction-Feeding Fishes: Identifying New Approaches to Performance Integration During Prey Capture in Aquatic Vertebrates

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Synopsis Organisms are composed of hierarchically arranged component parts that must work together to successfully achieve whole organism functions. In addition to integration among individual parts, some ecological demands require functional systems to work together in a type of inter-system performance integration. While performance can be measured by the ability to successfully accomplish ecologically relevant tasks, integration across performance traits can provide a deeper understanding of how these traits allow an organism to survive. The ability to move and the ability to consume food are essential to life, but during prey capture these two functions are typically integrated. Suction-feeding fishes have been used as a model of these interactions, but it is unclear how other ecologically relevant scenarios might reduce or change integration. To stimulate further research into these ideas, we highlight three contexts with the potential to result in changes in integration and underlying performance traits: (1) behavioral flexibility in aquatic feeding modes for capturing alternative prey types, (2) changes in the physical demands imposed by prey capture across environments, and (3) secondary adaptation for suction prey capture behaviors. These examples provide a broad scope of potential drivers of integration that are relevant to selection pressures experienced across vertebrate evolution. To demonstrate how these ideas can be applied and stimulate hypotheses, we provide observations from preliminary analyses of locally adapted populations of Trinidadian guppies (*Poecilia reticulata*) capturing prey using suction and biting feeding strategies and an Atlantic mudskipper (*Periophthalmus barbarus*) capturing prey above and below water. We also include a re-analysis of published data from two species of secondarily aquatic cetaceans, beluga whales (*Delphinapterus leucas*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), to examine the potential for secondary adaptation to affect integration in suction prey capture behaviors. Each of these examples support the broad importance of integration between locomotor and feeding performance but outline new ways that these relationships can be important when suction demands are reduced or altered. Future work in these areas will yield promising insights into vertebrate evolution and we hope to encourage further discussion on possible avenues of research on functional integration during prey capture.

Integration across performance traits

Organisms are composed of hierarchically arranged traits and component parts that must work together to successfully achieve whole organism functions (Seaborg 1999; Pepper and Herron 2008;

Ghalambor et al. 2015). The need for parts to successfully work together is often referred to as “functional integration,” where a functional outcome is the product of the integration (Fig. 1) (Olson and Miller 1951, 1958; Klingenberg 2014), and

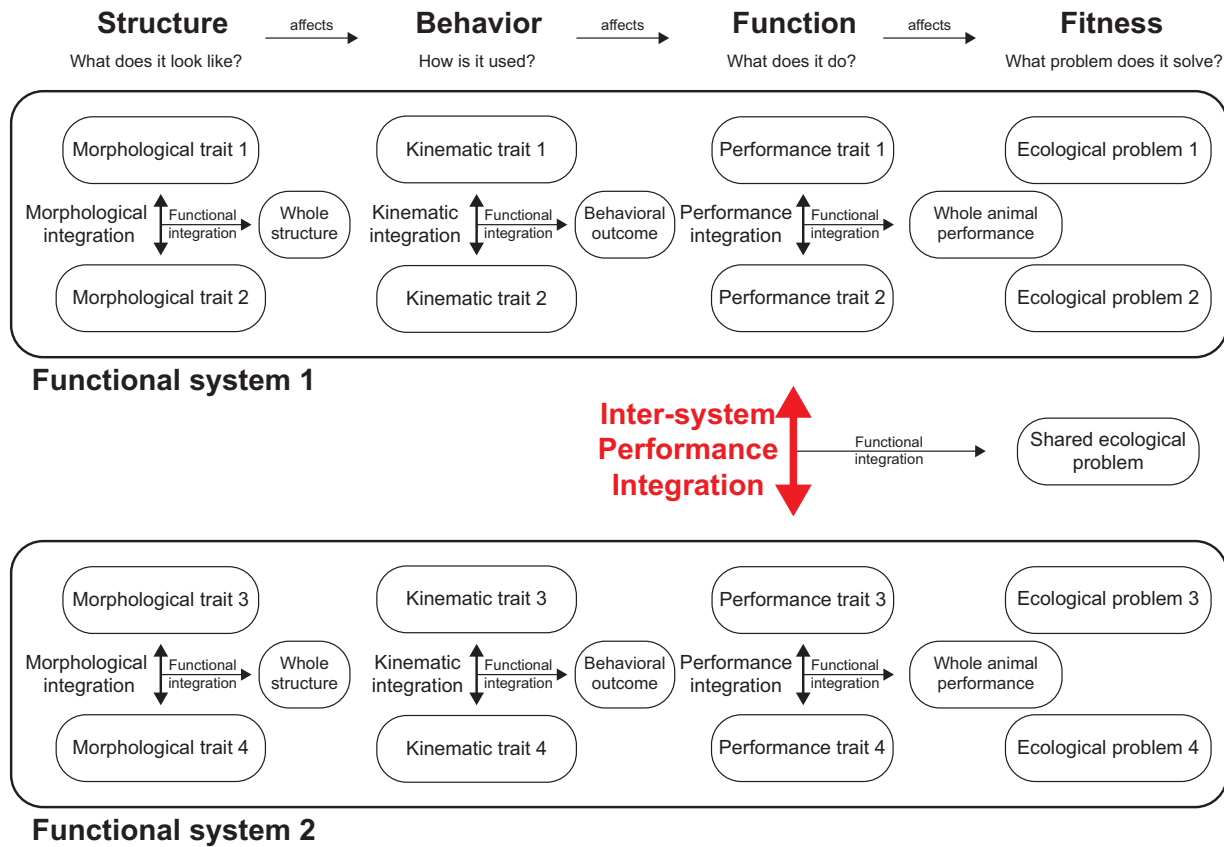


Fig. 1 A general framework for integration within and between functional systems. Multiple potential uses of the term “integration” occur, depending on the level of organization of interest. This terminology can be applied to multiple functional systems that generate potentially disparate performance outcomes. Performance integration can occur within a functional system as well as across functional systems. Our discussion of integration will center on that between performance outcomes across functional systems, or inter-system performance integration.

integration is identified using correlations to determine biological covariation (Olson and Miller 1951, 1958; Berg 1960; Gould and Lewontin 1979; Cheverud 1982; Pigliucci 2003; Wainwright et al. 2008). For example, changes in jaw and skull shape in cichlid fishes are correlated, and this integration provides the ability to better resist bite forces (Cooper et al. 2011). Without this integration, function may be compromised and success of the organism on both short (ecological interactions) and long (evolutionary) time scales may be negatively affected.

In addition to use of the descriptor “functional” to refer to a potential driver of integration, descriptors can also be applied to refer to the component parts that are integrated (Fig. 1). For example, “morphological integration” describes relationships between structural traits (i.e., What does it look like?) (Van Valen 1965; Cheverud 1982; Bastir and Rosas 2005; Klingenberg 2008; Goswami et al. 2014). Similarly, “kinematic integration” describes relationships between behavioral traits (i.e., How is it used?) that can be measured using motion

(Bishop et al. 2008; Montuelle et al. 2012b), and results in a behavioral outcome. For example, coordinated movement of limbs can result in forward propulsion. Performance is the ability to successfully accomplish ecologically relevant behavioral outcomes (i.e., What does it do?) (Irschick et al. 2008), and performance traits can also covary in an integrated way to produce new higher-order functions that are more directly related to survival and fitness than use of morphological or kinematic proxies. For example, many animals possess the capability to perform alternative “modes” of behaviors that require alternative kinematic patterns, but that can also be used together to facilitate a shared functional outcome. For example, suction and biting feeding modes in aquatic vertebrates each result from alternative kinematic patterns and behaviors, but can be combined during prey capture to compensate for an anteriorly projected bow wave (Summers et al. 1998; Ferry et al. 2015).

Despite the similarity in how these terms are applied across traits, differences in the traits themselves

have important implications for understanding higher-order functions of organisms (Wainwright 2007). Recognizing kinematic and performance integration as distinct from morphological integration is useful in three ways: (1) it distinguishes integration between traits that can be altered on short time scales in response to demand (performance) from integration between traits that are relatively static in the short term (structural features), (2) it recognizes potential differences between integration that results from active control by the central nervous system compared to forms that do not require this level of control, such as when integration results from mechanical linkages or shared developmental pathways (Wainwright et al. 2008; Kane and Higham 2015), and (3) it is variation in the use of structures, not necessarily their form, which supports new functions in the organism. In other words, multifunctional structures facilitate kinematic integration to accomplish new behavioral tasks. It is here where variation in how outcomes are achieved, rather than how structures are formed or used per se, that supports new solutions to ecological problems (Ferry et al. 2015). Therefore, examination of kinematic and performance integration, which have received less attention than morphological integration, can provide new insights into organism-level functions.

Another important viewpoint to consider when understanding organism function from a performance integration perspective is that due to the hierarchical nature of organismal traits, entire functional systems can also be integrated during common tasks (Pepper and Herron 2008; Klingenberg 2014). These functional systems can typically carry out disparate tasks on their own, but there may also be ecological demands that require these systems to work together in a type of inter-system performance integration (Fig. 1). For example, locomotor performance is frequently coupled with performance of other systems, such as sensory input (Falk et al. 2014, 2015; Mandecki and Domenici 2015), reproduction (Ghalambor et al. 2003, 2004), ventilation (Boggs 2002; Farmer and Carrier 2015), and feeding behaviors (Montuelle et al. 2012b; Kane and Higham 2015; Haines and Sanderson 2017). In this way, integration across functional systems represents a multistructural function, depending on structures and their usage that typically accomplish different tasks but can be performed together to support functions at the level of the whole organism. Throughout this article, the shorthand “integration” is used in reference to this level of integration across performance metrics of separate functional systems.

Suction-feeding in fishes is a useful model system to investigate these interactions, where the shared problem of approaching and capturing prey can be solved using integrated performance of locomotor and feeding systems in an emergent and non-additive way (Kane and Higham 2015). Here, we provide background on these ideas but propose that this is only a starting point for answering questions about inter-system performance integration and organism function since suction feeding represents an incomplete view of functional outcomes in either system. We examine how the context of the prey capture event can alter the functional demands on feeding and locomotor systems, potentially shifting the requirements for integration. In contrast to the idea that modulation of components affect higher-order functions (a “bottom-up” approach), we consider how changes in demand affect function, and the resulting changes in integration and component traits (a “top-down” approach). We draw on examples from our research laboratories to explore whether the integrated relationships observed during suction feeding remain relevant beyond the strict use of this behavior. Discussion of these examples is used to highlight similarities and differences compared to prior knowledge, and to inspire others to build on these ideas and develop research questions and hypotheses that can be tested in future work.

Suction-feeding in fishes as a model of performance integration

Many fishes rely on rapid expansion of their head and jaws to generate subambient intraoral pressure to draw water and prey into their mouth (Lauder 1985; Day et al. 2015; Wainwright et al. 2015); this involves multiple integrated components (Fig. 2). Fishes that rely on forceful suction (as experienced by the prey) typically have integrated morphological features (Wainwright 1996; Carroll et al. 2004; Collar et al. 2014; Day et al. 2015) whose integrated kinematic movements result in rapid wave of posteriorly directed mouth and head expansion (Gibb and Ferry-Graham 2005; Westneat 2006; Bishop et al. 2008; Collar et al. 2014; Day et al. 2015). Variation in related performance traits such as subambient force, strain rate, or ingested volume can result in feeding strategies tailored to capture alternative prey types (Holzman et al. 2008a, 2012). For example, a small, rapidly opening gape coupled with jaw protrusion maximizes force on attached prey, whereas a large, more prolonged gape, with or without protrusion maximizes engulfed volume and the chance of capturing large evasive prey (Higham et al. 2006;

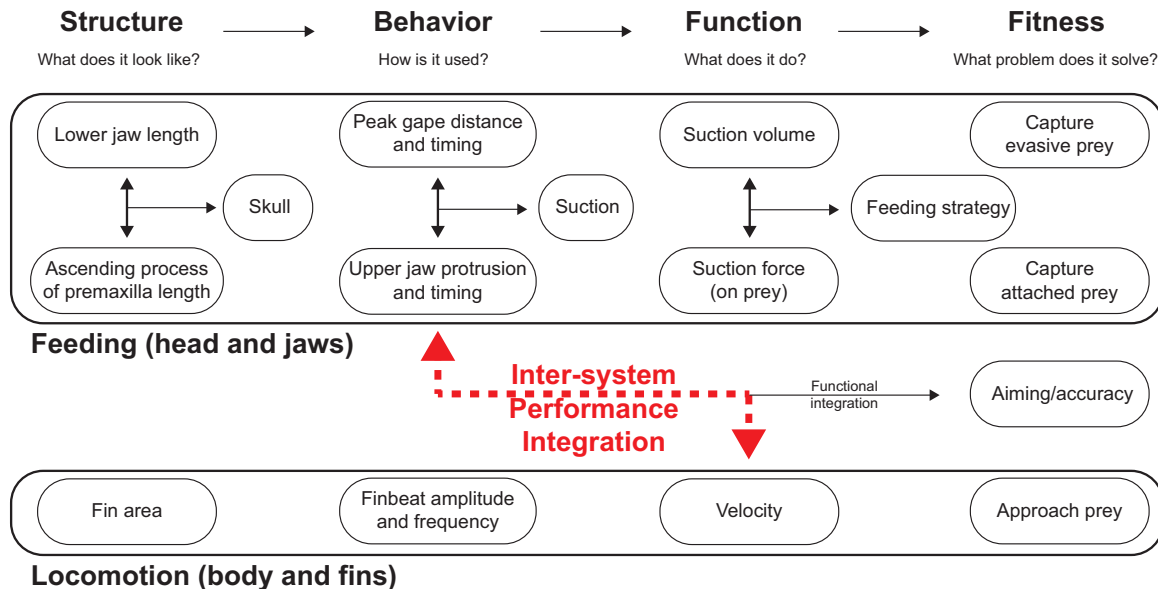


Fig. 2 An example of integration within the feeding functional system and across feeding and locomotor functional systems in fishes during prey capture. A simplified portrayal of the locomotor system is shown here due to the focus on feeding and prey capture. Due to empirical difficulty in quantifying suction performance (the flow of water into the mouth), function of the feeding system is often approximated using kinematics. Therefore, inter-system performance integration represents statistical correlation between cranial kinematics and locomotor performance outcomes such as velocity or changes in velocity. The hypothesized fitness outcome of these interactions is in aiming and accuracy during prey capture.

Holzman et al. 2007, 2008a, 2008b). The locomotor system similarly demonstrates integration among morphological, kinematic, and performance traits (Higham 2007a; Flammang and Lauder 2009; Langerhans 2009; Feilich 2016, 2017), but for brevity, those interactions are not the focus here and are simplified in Fig. 2.

In addition to integration within each of these functional systems, increasing evidence also suggests that integration across these systems can play a vital role during prey capture at structural, behavioral, and functional levels (Collar et al. 2008; Rice 2008; Tran et al. 2010; Camp et al. 2015, 2017; Larouche et al. 2015). We focus on integration across performance outcomes (higher-order functions) during whole-organism responses to prey since this has the most direct implications for survival. However, note that suction performance (metrics describing water flow into the mouth) is challenging to observe directly due to the need to visualize particles of water, and is often approximated in feeding trials using kinematics (Ferry-Graham et al. 2003; Day et al. 2005, 2007, 2015; Higham et al. 2006; Wainwright et al. 2007), whereas locomotor performance (metrics describing body translation such as approach speed) can be quantified directly. Mouth size, as an indicator of suction force experienced by the prey, and predator approach speed are broadly integrated during suction such that small mouths (forceful

suction) occur with slow swimming and large mouth size (high volume suction) occurs with faster swimming (Higham et al. 2006, 2007; Tran et al. 2010; Kane and Higham 2011; Oufiero et al. 2012; Kane and Higham 2015; Longo et al. 2015). This relationship may evolve in response to selection, but the mechanism is unclear at this time (Kane et al. 2019). Integration between locomotor and feeding performance is necessary so that the capture mechanism (suction volume and/or mouth) is placed in a precise and accurate location relative to the prey that maximizes capture success (Higham 2007b; Kane and Higham 2014). Therefore, inter-system performance integration is likely an important component of whole-organism function in suction feeding fishes. Although this idea is not necessarily new, many questions still remain and the details of this higher-order functional integration warrant further investigation.

One question that remains is how ecological problems that require alternative functions that deviate from suction can affect inter-system performance integration of locomotion and feeding during prey capture. Covariance between gape and approach speed during suction has been repeatedly demonstrated in suction-feeding fishes (reviewed in Kane and Higham 2015; Kane et al. 2019) but it is unclear if this relationship holds in other situations. Given the broad occurrence of suction during prey capture

in fishes (Wainwright et al. 2015), and the constraint of this feeding mode on skull form and function (Mehta and Wainwright 2007; Collar et al. 2014), integration with locomotion may similarly be constrained. In this case, integration of mouth size and swim speed may be constant in fishes such that it is present and relatively unchanging across species or contexts. However, changes in function may necessitate changes in underlying component traits and their integration. Fishes can behaviorally modulate both locomotor and feeding responses to prey based on contexts such as motivation, prey type, and environment (Nemeth 1997; Ferry-Graham et al. 2001; Sass and Motta 2002; Van Wassenbergh and De Rechter 2011; Gardiner and Motta 2012). Therefore, integration with locomotion during prey capture may also respond to changes in context, and may be more variable (within behaviors) and flexible (across behaviors; *sensu* Wainwright et al. 2008) than what can be, and has been, described between gape and approach speed during suction feeding. Therefore, we discuss how changes in prey capture that necessitate new functional outcomes affect performance integration across functional systems.

To encourage the expansion of studies on inter-system performance integration to new ecologically relevant scenarios beyond suction-feeding, we highlight three contexts with the potential to result in changes in integration and its underlying performance traits: (1) behavioral flexibility in aquatic feeding modes in response to capturing alternative prey types, (2) changes in the physical demands imposed by prey capture across environments, and (3) secondary adaptation for suction prey capture behaviors. These examples provide a range of potential changes in integration relevant to the changes observed across vertebrate evolution. We provide observations from preliminary or published work in our laboratories to support the broad importance of integration between locomotor and feeding performance in each of these contexts and highlight new insights that warrant further exploration. We hope these ideas will stimulate students and researchers to pursue each of these ideas more deeply in future studies.

Context 1: Changes in prey type necessitate alternative feeding modes

Suction-feeding is commonly used among fishes to draw external prey into the mouth, but this is only one end of a continuum of potential feeding modes (Ferry et al. 2015; Longo et al. 2015). An alternative that can be utilized in the absence of suction and

requires a change in performance is biting to remove prey from a substrate. Several independent lineages of fishes possess jaws adapted for maximizing forceful contact with the surface and removal of encrusted food items (Gibb et al. 2008; 2015; Konow et al. 2008; Hernandez et al. 2009; Price et al. 2010), which extend prey opportunities beyond those available using suction (Gibb et al. 2015) and demonstrate that structural changes can facilitate biting behaviors. However, even in the absence of structural modifications, kinematics and performance can also change. Whereas suction is dependent on mouth opening behaviors and indirect contact with prey to generate the suction volume and capture prey, biting relies on mouth closing behaviors and direct contact by the jaws to obtain and manipulate prey (Ferry et al. 2015; Kane et al. 2019). Additionally, performance is optimized using opposite kinematics; during suction, performance (force on the prey) is maximized when gape and opening duration are decreased (Higham et al. 2006; Holzman et al. 2007, 2008a; Wainwright and Day 2007; Day et al. 2015), but during biting, increased gape and opening duration permits increased contact with the surface and enhanced prey removal (Gibb et al. 2008; Konow et al. 2008). But how might these differences be reflected in integration with the locomotor system during prey capture?

Compared to suction-feeding, integration with locomotion during biting is less well understood. If coordination of approach speed and mouth size is an applicable constraint beyond suction behaviors, such as in avoiding collision, then integration may be present regardless of the prey type consumed. However, biting does not rely as heavily on intracranial integration within the feeding system (Collar et al. 2014) and can be performed in a range of situations, potentially even facilitating transitions between aquatic and terrestrial environments (Marshall et al. 2008, 2014, 2015). Additionally, biting in fishes occurs when prey are relatively non-evasive or large, potentially reducing the reliance on locomotion and allowing flexibility among component traits (Ferry et al. 2015). Therefore, integration during biting may be weakened to facilitate alternate prey capture strategies (Webb 1984; Kane and Higham 2015).

To begin to examine how changes in prey type might affect integration and performance in the same individual, we present new observations of locally adapted populations of Trinidadian guppies (*Poecilia reticulata*) capturing prey using suction and biting feeding strategies and compare these to previously published data for guppies using suction-feeding (Kane et al. 2019). Guppies have repeatedly

Table 1 Summary statistics for guppy performance data

Behavior		Biting		Suction		t-test (feeding mode)	
		High predation	Low predation	High predation	Low predation	High predation	Low predation
Population							
Number of individuals		8	8	6	7		
Standard length (cm)	Mean	2.408	2.631	2.809	3.042	$t = 4.167$	$t = 2.90$
	SD	0.219	0.330	0.140	0.214	$P = 0.0014^*$	$P = 0.0132^*$
	Min	2.154	2.031	2.658	2.693		
	Max	2.741	2.996	2.985	3.307		
95% peak gape (cm)	Mean	0.224	0.250	0.230	0.205	$t = 0.415$	$t = -2.048$
	SD	0.032	0.026	0.019	0.053	$P = 0.6859$	$P = 0.0726$
	Min	0.187	0.200	0.215	0.134		
	Max	0.268	0.283	0.266	0.291		
Peak approach speed ^a (cm/s; from mouth opening to 95% peak gape)	Mean	2.488	2.075	3.604	2.925	$t = 1.125$	$t = 1.596$
	SD	1.249	0.875	1.415	1.033	$P = 0.2878$	$P = 0.1393$
	Min	1.035	1.253	1.431	2.042		
	Max	4.170	3.876	4.927	4.874		

^aCalculated from mouth opening to peak gape (substrate contact) for biting and mouth opening to mouth closing during suction behaviors.

*Statistically significant at $P < 0.05$.

colonized upstream low predation (LP) environments from downstream high predation (HP) populations, resulting in shifts from predator-driven to density-dependent natural selection (Reznick and Endler 1982; Endler 1995; Bassar et al. 2013). This divergence has resulted in correlated changes in trophic ecology (Palkovacs et al. 2011; Zandonà et al. 2011; 2017), predator escape performance (O'Steen et al. 2002; Walker et al. 2005; Dial et al. 2016), and integration of swim speed and gape during prey capture (Kane et al. 2019). Specifically, when using suction to capture live zooplankton prey (wild-type cladocerans and copepods), inter-system performance integration occurs repeatedly in LP environments but is absent in HP ancestral populations (Kane et al. 2019). Although they can use suction, guppies, like other Poeciliid fishes, use a specialized jaw morphology to perform biting behaviors and biting plays a significant role in the feeding strategy of these fish (Dussault and Kramer 1981; Gibb et al. 2008; Hernandez et al. 2009; Zandonà et al. 2011, 2017). Therefore, we use guppies as a model system to ask how an alternative prey capture strategy might alter integration of gape and approach speed compared to suction.

New observations of fish performing both prey capture strategies were obtained by recording guppies at 500 frames/s capturing live, wild-captured plankton prey in the water column (suction) or feeding upon a vertical agar substrate (biting). Only a single HP/LP population pair from the Aripo River

(six to eight individuals each population and behavior) is included here because these populations replicate those from previous work (Kane et al. 2019). The tips of the jaws and approximate center of mass were digitized from the single best video for each fish to calculate 95% peak gape and peak approach speed during the feeding behavior. Previous work used 100% peak gape and approach speed at the time of peak gape (Kane et al. 2019), and differences here are to standardize traits across suction and biting behaviors. We use gape as a proxy for both suction performance (small mouth size indicates greater suction force) and biting performance (large gape indicates greater bite area). Differences in performance were described using t -tests and integration was determined using correlations between gape and approach speed. Additional methods are described in the [Supplementary data](#).

In our new sample of guppy feeding data, population of origin may have had a greater influence on integration than prey capture strategy. Body size was larger during suction-feeding trials due to the later filming date. However, approach speed and peak gape were similar across prey capture behaviors (Table 1). Gape was relatively large and independent of prey capture strategy, which supports the idea that guppies tend to show reduced ability to generate forceful subambient pressures, but an increased ability to contact the substrate for biting. Compared to trials analyzed in previous work (Kane et al. 2019), the newly analyzed data show approach speeds were

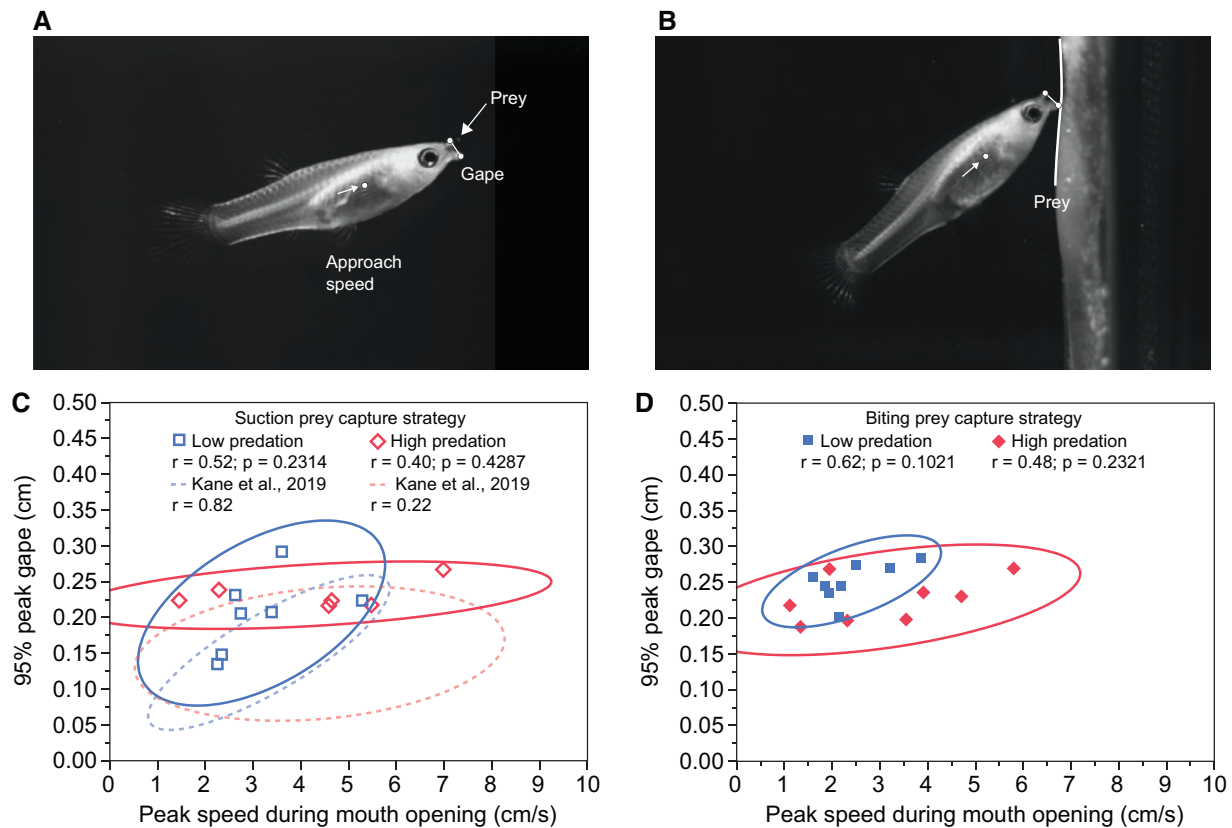


Fig. 3 Prey capture behaviors (A, B) and their integration (C, D) for HP (red diamonds) and LP (blue squares) guppies (*P. reticulata*) using suction (A, C, unfilled shapes) and biting (B, D, filled shapes) prey capture strategies. Still frames are shown at the time of 95% peak gape and prey location is indicated. Performance traits were determined using gape representative (distance between upper and lower jaws) and approach speed (rate of change in position of the approximate center of mass). The 95% density ellipse is shown for each population and behavior and correlation statistics are provided. Correlation ellipses from previous work on integration during suction in guppies (Kane et al. 2019) are also shown for comparison (C). Integration during suction was not replicated, (see discussion in text). However, the magnitude of the correlation for the current data is consistently higher for LP fish during both prey capture behaviors compared to HP fish, a pattern that trends toward that in prior work, suggesting that similar patterns of integration may span alternative prey capture strategies in guppies.

similar but gape may have been slightly larger (Fig. 3C). Interestingly, the magnitude of potential correlations were consistently greater for LP populations (Fig. 3C,D), suggesting that divergence across HP/LP populations may be a stronger influence on integration than divergence due to prey capture strategy. However, in contrast to previous work, correlations between performance traits were weaker and not statistically significant in our new samples (Fig. 3C,D), suggesting either an inability to detect integration (likely due to a small sample size) or a general lack of integration overall. Excluding sample size, several differences between the previous and current samples of guppies may have also contributed to this difference in strength of integration, including but not limited to random differences in guppy and/or prey populations across sites or year of sampling and/or random differences in housing or experimental equipment across different labs.

Further investigation is needed to tease apart the effects of these possible factors.

The preliminary comparisons of guppy feeding events presented here may be limited in their ability to provide conclusive support, but do suggest that further work examining the potential for changes in inter-system performance integration, is warranted. In this case, the type of prey being captured imposes alternate demands on locomotor and feeding functional systems, but this may not be sufficient to significantly alter performance or its integration when alternate capture strategies are performed within the same individuals using the same structural traits. Alternatively, differences that have evolved between HP and LP populations may play a larger role in affecting structures, their use, and their integration during prey capture. The current discussion is limited to guppies, but experiments involving alternate biting and suction capture strategies more broadly

across fishes can further explore how shifts in specialization for each strategy may lead to potential differences in integration.

Context 2: Alternate physical demands during prey capture

The physical differences between water and air are a known driver that explains divergence in feeding kinematics and prey capture strategies in a variety of vertebrates (Shaffer and Lauder 1988; Reilly 1996; Summers et al. 1998; Vincent et al. 2005; Marshall et al. 2008, 2014, 2015; Natchev et al. 2009; Van Wassenbergh 2013; Hocking et al. 2014; Michel et al. 2015a, 2016). However, it is not well understood how these changes might impact integration across functional systems. Since water is denser and more viscous than air, it imposes significant challenges to movement (i.e., drag) that are minimized in terrestrial environments. However, on land, propulsion also includes counteracting the effects of gravity on body mass. These differences have implications primarily for locomotion but also for feeding behaviors such as suction, which relies on the density and viscosity of water and cannot be accomplished on land (but see Michel et al. 2015b). Because of these differences, amphibious vertebrates often switch locomotor or feeding modes across environments (O'Reilly et al. 2000; Ashley-Ross and Bechtel 2004; Van Wassenbergh 2013; Michel et al. 2016; Heiss et al. 2018), potentially affecting integrated relationships between these systems. Alternatively, challenges inherent in predator-prey interactions may supersede those presented by the environment, and integration of locomotion and feeding may be similar across environments. For example, lunge behaviors that utilize a rapid burst of forward movement toward prey can be performed in water and air, despite differences in the mechanism of propulsion in each medium. Therefore, if the functional outcome is similar across environments, locomotion and feeding may be integrated in a way that is independent of specific kinematic or performance traits in each system.

Understanding whether and how differences in prey capture in water versus air affect integration between locomotor and feeding performance requires comparisons among animals attempting prey capture across both of these environments. Integration has been described separately in aquatic teleost fishes and terrestrial squamate lizards (Higham 2007b; Higham et al. 2006, 2007; Montuelle et al. 2009, 2012a, 2012b; Kane and Higham 2011; Kane and Higham 2015; Kane et al. 2019). In both taxa, feeding (head and jaw) and

locomotor (body and limb) movements are important for integration, but it is unclear whether differences reflect those between species or prey capture environments. Therefore, examining integration in amphibious organisms that can capture prey in both aquatic and terrestrial environments can provide a useful avenue for teasing apart evolutionary and environmental differences in prey capture and integration. Mudskippers (Order Gobiiformes, Family Oxudercidae) are one such group within which comparisons across prey capture environments are possible. In this group of fishes, the ability to generate subambient pressures is likely compromised in water (Michel et al. 2014) such that the feeding system may perform a relatively similar biting behavior in and out of water. However, the propulsive system may be more flexible across environments, switching between structures and modes of locomotion with changes in demand (Pace and Gibb 2009). Therefore, differences in kinematics and performance of the locomotor system across terrestrial and aquatic environments may result in different patterns of inter-system integration than what is observed during suction prey capture in strictly aquatic feeders.

To begin to provide insight into potential changes in locomotion and feeding during prey capture in amphibious animals and stimulate further research, we present observations of an Atlantic mudskipper (*Periophthalmus barbarus*; 13.1 cm standard length) prey capturing on land (in air) and in water. A single individual was recorded at 500 frames/s capturing thawed bloodworms from an acrylic sheet wrapped in a paper towel, either floating on a polystyrene sheet above water or submerged underwater. The eye, tips of the jaws, and prey were digitized in 10 land and 9 water trials to determine body velocity, gape, and distance to the prey as a measure of accuracy. *t*-tests were used to compare performance traits across environments and correlations between these variables were used to determine the likelihood of inter-system performance integration. Additional information on methodology is available in the [Supplementary data](#).

Despite similar reliance on a lunge behavior toward prey in both environments, component behavioral traits and their integration likely differ between terrestrial and aquatic environments in a mudskipper (Fig. 4). On land, the mudskipper relied on a laterally pronated caudal fin and/or depression and retraction of pectoral fins to rotate its body over the stationary pelvic fins, similar to “crutching” movements that have been reported in amphibious fishes moving on land (Stebbins and Kalk 1961; Sayer 2005; Pace and Gibb 2009; Ashley-Ross et al. 2013;

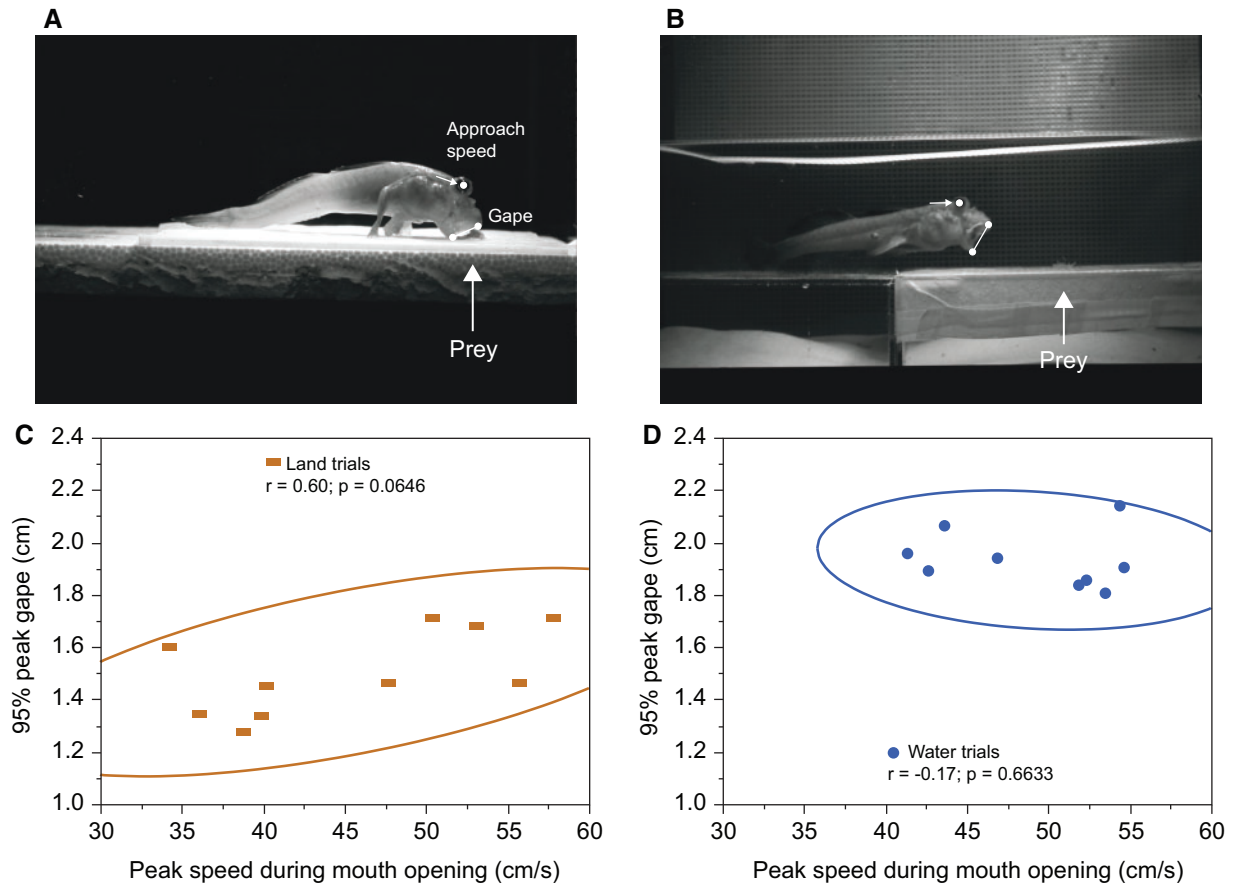


Fig. 4 Prey capture behaviors (**A, B**) and their integration (**C, D**) for a mudskipper (*P. barbarus*) capturing prey in a terrestrial (**A**, orange rectangles) and aquatic (**B**, blue circles) environment. Still frames are shown at the time of 95% peak gape and prey location is indicated with an arrow. Performance traits were determined using gape (distance between upper and lower jaws) and approach speed (rate of change in position of the eye). The 95% density ellipse is shown for each environment and correlation statistics are provided. On land, the fish performed a lunge via rotation over the pelvic fins whereas in water a lunge was achieved by generating forward thrust with the pectoral fins. Aiming was poor in water and the integrated relationship was weaker. These data are preliminary and represent a single individual but suggest the importance of further exploration of these trends.

Kawano and Blob 2013). In water, the mudskipper continuously swam in the direction of the prey with a horizontal trajectory, without contacting the substrate, and relied on multiple propulsive strokes of the pectoral fins. In water, prey moved into the mouth as a result of suction generated in water, despite being potentially limited in this ability morphologically (Michel et al. 2014). On land, prey movement was not observed and prey were captured using direct contact with the jaws. Gape was consistently larger in water than on land but approach speed was similar in both environments (Table 2). A larger gape may be the result of the pressure of the water forcing the jaws open to a greater extent, similar to the mechanism responsible for rapidly increasing gape in Balaenopterid lunge-feeding whales (Goldbogen et al. 2015). Aiming was generally poor in water (Table 2), in contrast to observations in a

Table 2 Summary statistics for mudskipper performance data

Environment		Land	Water	t-test
Number of trials		10	9	(environment)
95% peak gape (cm)	Mean	1.50	1.93	$t = 6.81$
	SD	0.16	0.11	$P < 0.0001^*$
	Min	1.28	1.81	
	Max	1.71	2.14	
Peak approach speed (cm/s; from mouth opening to 95% peak gape)	Mean	45.4	49.0	$t = 1.11$
	SD	8.6	5.4	$P = 0.2821$
	Min	34.3	41.4	
	Max	57.8	54.7	
Distance from prey to predator eye at 95% peak gape (cm)	Mean	2.33	8.42	$t = 10.63$
	SD	0.11	1.72	$P < 0.0001^*$
	Min	2.22	6.08	
	Max	2.47	11.76	

*Statistically significant at $P < 0.05$.

previous study (Michel et al. 2016). This difference may be due to subject being only partially submerged in prior work, allowing their visual system to operate in air where visual acuity is increased (Sponder and Lauder 1981; Sayer 2005). Combined, the differences observed here in locomotor and feeding performance resulted in stronger integration when behaviors were performed on land (Fig. 4). Although statistical significance was not achieved, likely due to the variation present within our small sample, the magnitude of the potential correlation during land trials ($r=0.6$) is similar to correlations observed during suction feeding ($r=0.5-0.8$) (Higham 2007a; Tran et al. 2010; Kane et al. 2019), suggesting this trend may hold upon further examination in future work. In contrast, the potential correlation during water trails ($r=-0.17$) is much closer to 0, indicating that these trials most likely lack integration. Therefore, this preliminary evidence suggests that integration between gape and approach speed may be present, but only during prey capture on land, in contrast to its presence in water for solely aquatic suction feeding fishes.

The results presented here are limited in scope, but suggest that further work investigating inter-system performance integration in amphibious organisms, where the medium within which prey capture occurs imposes alternate demands on functional systems, is merited. In these animals, the same structural components are utilized to perform different within-system functions and as a result, integration may differ in ways not observable in suction feeding fishes. Additionally, these preliminary results suggest that the ability to integrate performance systems may be affected both by the media within which prey capture occurs acting on locomotor and feeding structures, and sensory capabilities in each environment. Integration of kinematic and performance traits is likely determined by active neuro-mechanical coordination (Wainwright et al. 2008; Kane and Higham 2015), such that changes in the ability to detect prey might limit the ability to integrate the approach with mouth opening to achieve successful capture. Future work is needed to better understand the contributions of sensory input to integrated performance behaviors.

Context 3: Secondary adaptation to aquatic prey capture

One of the most extreme examples of convergence has occurred in several lineages of terrestrial vertebrates that have secondarily returned to an aquatic

environment. Convergence occurs when groups of organisms evolve similar responses to common selective pressures, despite divergent evolutionary history (Losos et al. 1998; Rüber and Adams 2001; Serb et al. 2011). Due to the strong selective forces of a dense and viscous aquatic environment, many secondarily aquatic vertebrates have evolved prey capture strategies that are analogous to those found in fishes (Bryden 1988; Thewissen et al. 1994; Fish 1998; Thewissen 1998). One such character is the ability to use subambient pressure (suction) to capture prey (Stinson and Deban 2017). In secondarily aquatic animals, the gill chambers have been lost, the suction volume is limited to that of the mouth cavity, and water has the potential to flow back out of the mouth while it is still being sucked in (Lauder and Shaffer 1986; Lauder and Reilly 1988; Reilly and Lauder 1988; Deban and Wake 2000; Stinson and Deban 2017; Heiss et al. 2018). Therefore, structural accommodations are necessary to compensate for these constraints to produce the same functional output as observed fishes (Stinson and Deban 2017).

Some marine mammals such as cetaceans and pinnipeds are specialized for suction generation (Marshall and Goldbogen 2015). Innovations that facilitate this prey capture mechanism include a vaulted palate and a large, wide hyolingual apparatus (Bloodworth and Marshall 2005; Marshall et al. 2008, 2014, 2015; Kane and Marshall 2009; Hocking et al. 2013; Marshall and Goldbogen 2015; Marshall and Pyenson 2019; Reidenberg and Laitman 1994; Werth 2007), as well as modified short and wide orofacial morphology that often uses lip pursing to occlude lateral gape and form a circular mouth aperture (Werth 2006; Marshall et al. 2008, 2014, 2015; Kane and Marshall 2009; Marshall and Goldbogen 2015; Marshall and Pyenson 2019). These morphological adaptations can result in suction performance comparable to primarily aquatic fishes (Kastelein et al. 1994, 1997; Werth 2000; Marshall et al. 2008, 2014, 2015; Kane and Marshall 2009). However, it is unclear whether integration with the locomotor system may be similar to suction feeding fishes as well.

Although suction specialists may be able to generate significant subambient pressures, many secondarily aquatic species may still experience constraints that limit the use of suction for prey capture (Stinson and Deban 2017), which may have consequences for integration with locomotion. A reduced ability to draw prey into the mouth using suction necessitates an increased reliance on body movement to position the mouth close to the prey (Kane and Higham 2014), imposing constraints on the use of locomotion and its integration with feeding. In fact,

the greatest suction pressures have been recorded from secondarily aquatic tetrapods during behaviors that constrain locomotion (i.e., feeding from a stationary device) or when forward velocity is significantly reduced (Bloodworth and Marshall 2005; Marshall et al. 2008, 2014, 2015; Kane and Marshall 2009; Hocking et al. 2013). These species are typically feeding on benthic prey. Alternatively, species that rely more on locomotion during prey capture may use suction only in a compensatory manner that counteracts the bow wave generated during forward movement, and not as a primary method of closing distance to the prey (Lauder and Prendergast 1992; Summers et al. 1998; Bloodworth and Marshall 2007; Kane and Marshall 2009). This dichotomy suggests that the integrated relationship between approach speed and gape described in suction feeding fishes (Kane and Higham 2015; Kane et al. 2019) may also be apparent in secondarily aquatic animals to some degree. Therefore, we ask how secondary adaptation to aquatic prey capture affect patterns of inter-system integration compared to relationships observed during suction prey capture in primarily aquatic feeders.

We re-analyzed published kinematic data (Kane and Marshall 2009) from two species of secondarily aquatic cetaceans to examine the potential for intra-system performance integration during aquatic prey capture (see [Supplementary Methods](#) for further details). Beluga whales (*Delphinapterus leucas*) rely on suction generation to pull prey toward the mouth for capture, whereas Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) use a raptorial biting, ram strategy to overrun prey in combination with compensatory suction (Fig. 5). As with the previous examples, we use correlations between peak gape and peak approach speed (from mouth opening through closing) to determine the presence of intra-system performance integration during prey capture in cetaceans.

For both species, the correlation between feeding and locomotor traits was statistically significant ($P < 0.05$), indicating the presence of integration between functional systems (Fig. 5). In belugas, this correlation ($r = 0.518$) is within the range of values reported in suction feeding fishes ($r = 0.5–0.589$) (Kane et al. 2019). The ability to achieve integration comparable to suction feeding fishes despite the vast divergence between taxa suggests that integration using this strategy may depend more on performance outcomes than the underlying structures and behaviors that generate performance. However, the correlation between gape and speed is negative in Pacific white-sided dolphins. This is in contrast to

theoretical and reported relationships between these variables during suction-feeding in fishes (Higham et al. 2007; Higham 2007b; Kane and Higham 2015; Kane et al. 2019; Montuelle and Kane 2019). This includes ram-suction feeding largemouth bass ($r = 0.762$) with a greater observed swim speed during prey capture (Higham 2007a) similar to Pacific white-sided dolphins. However, bass tend to rely on high-volume suction (Higham et al. 2006) whereas Pacific white-sided dolphins rely on compensatory suction, where both volume and velocity of suction may be weaker. Therefore, this negative relationship between locomotion and feeding in at least one species of secondarily aquatic vertebrate may represent a novel form of inter-system performance integration that has not been described in aquatic-feeding vertebrates previously.

The potentially novel relationship between feeding and locomotor functional systems in Pacific white-sided dolphins may be a reflection of secondary adaptation to an aquatic lifestyle imposing a constraint on integration. Marine mammals demonstrate remarkable convergence in form and function with fishes in both swimming and feeding (Fish 1996; Marshall and Goldbogen 2015; Pabst 2015). However, without structural and behavioral modifications for specialized performance, as in belugas, (Kane and Marshall 2009), convergence in integration across functional systems may not be possible. Ram-feeding fishes that rely on swim speed to overtake prey (i.e., largemouth bass) open their opercular cavities earlier in the gape cycle than those relying on suction (Muller et al. 1980; Muller and Osse 1984; Van Leeuwen and Muller 1984; Van Wassenbergh 2015). This allows water to flow unidirectionally through the mouth to minimize resistance (drag) during the mouth opening phase (Ferry et al. 2015). Marine mammals lack a gill chamber and therefore likely encounter significant drag and/or a bow wave during ram feeding behaviors. Lunge feeding whales can utilize this drag to rapidly increase gape during their feeding events (Goldbogen et al. 2007), or have evolved a channel at the posterior margin of the jaws that allows water to exit the mouth cavity unidirectionally during continuous ram filter-feeding (Goldbogen et al. 2015). Similarly, harbor seals, and potentially belugas, can expel water posteriorly using flexible lips (Kane and Marshall 2009; Marshall et al. 2014). Pacific white-sided dolphins, like most dolphins, do not have this morphological structure and may be forced to minimize gape at high speed to reduce drag, resulting in the negative correlation with speed observed here.

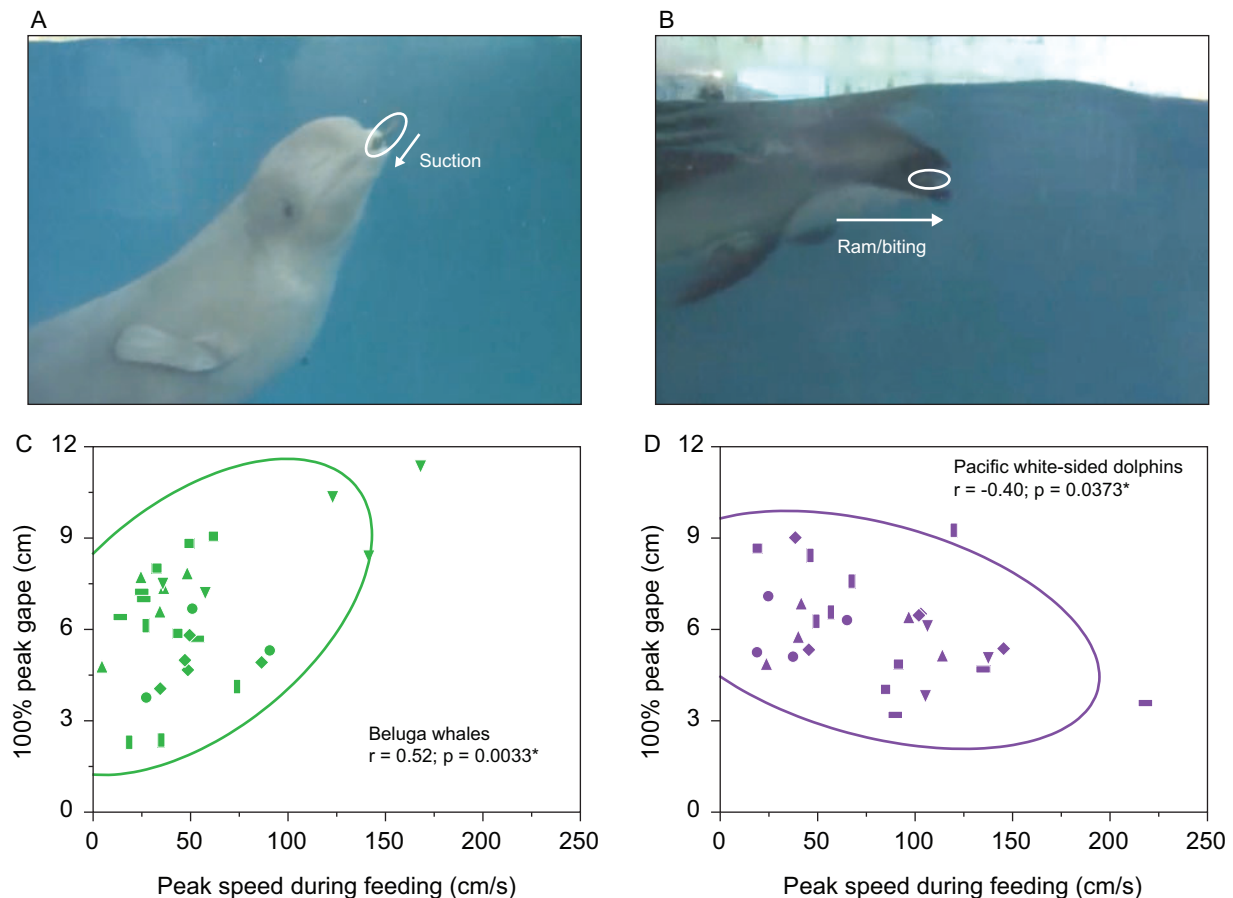


Fig. 5 Integration of locomotor and feeding performance during prey capture in secondarily aquatic beluga whales (**A, C**, green shapes) and Pacific white-sided dolphins (**B, D**, purple shapes). Prey are circled and the more prominent movement is indicated with an arrow on the still images taken from representative videos, indicating the use of different feeding modes in each species. Integration is represented by correlations of peak gape (feeding) against peak speed during feeding (locomotion) (**C, D**). Different individuals are shown with contrasting shapes and the 95% density ellipse is shown for each species. Correlation statistics are shown and statistical significance at the $P < 0.05$ value is indicated with an asterisk. Integration is present in both species but Pacific white-sided dolphins show a negative correlation between peak gape and peak speed, differing from belugas and previously described relationships in suction feeding fishes.

The results presented here provide deeper insight into the possibility for convergence and constraint in integrated relationships between locomotor and feeding systems and suggest that further work examining convergence in form and function of integration would provide new insights into the drivers of vertebrate feeding strategies and their evolution. In animals that display convergence, function is retained despite differences in form, highlighting the importance of integration at higher levels of organization for maintaining whole-organism function. However, in other vertebrates, function is divergent and new ways of integrating functional systems may be necessary. These hypotheses should stimulate further work examining the role of secondary convergence on integration across functional systems.

Conclusions

Each of these alternative prey capture contexts and the examples and observations highlighted in this work support the broad significance of integration between functional systems during prey capture in a wide range of aquatic vertebrates. But these observations also suggest ways in which integration might change as a response to changes in ecological demand that result in reduced or altered reliance on suction. These examples also highlight that integration of performance across functional systems may represent new ways of understanding how components of an organism work together to achieve common goals, compared to more traditional studies of morphological integration. Through the addition of

components that can be altered on short time scales (compared to morphology) we have the opportunity to understand the compounding and hierarchical effects of integration on organism function.

These examples are only a starting point for further inquiry and additional contexts besides those presented in detail here may also affect performance and its integration. Little is known of integration in terrestrial vertebrates (Montuelle et al. 2008, 2009, 2012a, 2012b), where both the structures generating performance and the performance itself can be vastly different compared to in an aquatic medium. Additionally, sensory systems likely play a large role in the ability to detect stimuli and perform appropriately integrated tasks (Birn-Jeffery and Higham 2016; Higham and Schmitz, 2019). We encourage other researchers to continue expanding beyond the examples provided here to continue exploring how traits are integrated and how this relates to changes in environmental demand.

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Supplementary data

Supplementary data available at *ICB* online.

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