The Journal of Experimental Biology 214, 1092-1099
© 2011. Published by The Company of Biologists Ltd
doi:10.1242/jeb.052068

RESEARCH ARTICLE

The integration of locomotion and prey capture in divergent cottid fishes: functional disparity despite morphological similarity

Emily A. Kane* and Timothy E. Higham

Clemson University, Department of Biological Sciences, Clemson, SC 29634, USA

*Author for correspondence (ekane@clemson.edu)

SUMMARY

Many mobile animals rely on the integration of locomotion and feeding to capture prey. Fishes commonly swim up to a prey item and utilize a combination of ram and suction feeding for prey capture. Marine cottids represent a diverse and abundant lineage of fishes that exhibit variation in feeding mode that is related to their mouth morphology. However, little is known regarding the integration of the locomotor and feeding systems during prey capture. We quantified the feeding kinematics, feeding performance and integration of locomotion and feeding in two species of divergent cottids: *Blepsias cirrhosus* (silver-spotted sculpin) and *Oligocottus maculosus* (tidepool sculpin). Individuals were caught from sympatric habitats near the Bamfield Marine Sciences Centre on Vancouver Island and filmed with a high-speed video camera (500 Hz) while feeding on amphipod prey. Two principal component axes summarize differences in integration and feeding mode despite similarity in attack velocity and feeding morphology (peak gape, peak cranial elevation and peak jaw protrusion). A greater number of correlations between locomotor and feeding variables in *B. cirrhosus*, compared with *O. maculosus*, indicate greater integration. We conclude that traditional measures of attack kinematics do not capture functionally and ecologically relevant differences between species. The mechanisms underlying differences in locomotor strategy likely result from unexplored morphological or ecological differences between species. In cottids, integration is apparent in more basal, subtidal species such as *B. cirrhosus*, and the need for integration may be superceded by demands from the habitat in more derived, shallow-water species such as *O. maculosus*.

Key words: *Blepsias cirrhosus*, *Oligocottus maculosus*, suction feeding, ram feeding, kinematics, acceleration profile.

INTRODUCTION

Many vertebrates rely on their locomotor system in order to successfully capture prey, including fishes (Nyberg, 1971; Nemeth, 1997; Rice and Westneat, 2005; Higham, 2007b; Rice, 2008), amphibians (Hoff et al., 1985; Gray and Nishikawa, 1995; Dean, 2003), reptiles (Irschick and Losos, 1998; Alfaro, 2003; Montuelle et al., 2009), birds (Shifferman and Eilam, 2004) and mammals (Dunbar and Badam, 2000; Goldbogen et al., 2007; Kane and Marshall, 2009). Although aquatic animals can capture prey by biting (Bellwood and Choat, 1990), prey capture in fishes commonly incorporates suction and ram (swimming) feeding. Whereas ram feeding relies on predator speed to overtake the prey (Liem, 1980; Norton and Brainerd, 1993), suction feeding relies on rapid expansion of the buccal cavity to draw prey towards the predator (Muller et al., 1982; Muller and Osse, 1984). However, suction is useful only over limited distances (Svanback et al., 2002; Day et al., 2005) and fishes often combine suction with ram feeding so that most species fall along a continuum between pure suction and pure ram. Metrics have been established to assess species performance in these categories. For example, suction feeding performance can be related to the rate at which the mouth expands (Day et al., 2005; Higham et al., 2006a), but also to the size and timing of maximum gape.

Although suction is a pervasive mechanism for capturing prey in aquatic vertebrates (Lauder, 1985), this strategy can be less efficient when capturing evasive prey (Nyberg, 1971; Norton, 1991; Nemeth, 1997), and ram feeding is often combined with suction feeding to take advantage of prey resources (Liem, 1980; Norton, 1991; Wainwright et al., 2001). Webb (Webb, 1984b) noted that locomotor behavior can influence prey capture success and feeding mode, and recently, aspects of the locomotor system have been linked to performance of the feeding system (Higham, 2007a). This link between locomotion and feeding indicates that a specific combination of locomotor and feeding behavior is important to successfully capture prey. Integration of these two systems is therefore important for defining feeding strategy.

Studies examining the integration of locomotion and feeding in fishes have typically focused on fishes that swim with their median and paired fins (MPF) including centrarchids (Higham et al., 2005; Higham, 2007b), cichlids (Higham et al., 2007) and labrids (Rice and Westneat, 2005; Collar et al., 2008; Rice, 2008; Rice et al., 2008). Among centrarchids and cichlids, for example, smaller peak gapes are typically correlated with slower swimming speeds and increased strike accuracy (Higham et al., 2006b; Higham et al., 2007). Additionally, pectoral fins can be used not only to decelerate during prey capture (Webb and Skadsen, 1980; Rand and Lauder, 1981; Geerlink, 1987; Higham, 2007b; Rice, 2008), but also for increased maneuverability (Gerstner, 1999; Higham, 2007a). Because locomotor performance during prey capture can influence prey capture success and feeding strategy, understanding how locomotion and feeding are integrated will allow us to better understand the consequences and origins of morphological and functional diversity in fishes that rely on both systems to successfully capture prey.

Marine cottid fishes (Scorpaeniformes: Cottidae) from the northeastern Pacific Ocean are ideal for studies of predator–prey interactions as they are abundant, morphologically diverse and exhibit a large degree of diet diversity (Yoshiyama, 1980; Strauss and Fuiman, 1985; Norton, 1991; Norton, 1995). Because of this, they make up an important part of the intertidal and subtidal fauna in the Northeast Pacific. Cottids have been described as locomotor

specialists for body and caudal fin (BCF) transient locomotion, with a body form that maximizes thrust. Cottids have also been characterized as benthic specialists, as their pectoral fins are adapted for holding position on the substrate in flowing water (Gosline, 1994; Webb et al., 1996). The wide variety of habitat type occupied by cottids, ranging from deep subtidal to tidepools and freshwater systems, results in a wide diversity of morphology that can be correlated to diversity in function. For example, small-mouthed species use suction to capture non-evasive prey items (Norton, 1991; Norton, 1995). However, some species demonstrate inconsistent results, indicating that other potentially important variables, such as the integration of locomotion during prey capture, are important. Additionally, it is unclear whether more atypical cottids demonstrate the link between morphology, feeding strategy and prey ecology.

Silver-spotted sculpins [*Blepsias cirrhosus* (Pallas 1814)] and tidepool sculpins (*Oligocottus maculosus* Girard 1856) share many similarities that would suggest similarity in feeding strategy. *Oligocottus maculosus* can be found sympatrically on the benthos of the same shallow subtidal pelagic habitats as *B. cirrhosus* (Jaenicke et al., 1985), where both species naturally feed on amphipods (Nakamura, 1971; Norton, 1995; Kolpakov and Dolganova, 2006). This prey type is typical for cottids that rely on suction (Norton, 1991) and indicates that both species should rely on similar feeding modes to capture prey. Additionally, because cottids are specialized for BCF propulsion, both species should display some reliance on ram feeding during prey capture. However, despite these similarities, *B. cirrhosus* are unlike typical cottids in that they inhabit kelp canopies and eelgrass beds, where they actively swim and only occasionally perch on the vegetation (Marliave, 1975). Therefore, a greater reliance on pelagic swimming in *B. cirrhosus* suggests better control over the locomotor system, which might allow for tighter integration of the locomotor system with feeding, and would provide insight into the consequences of diversity in cottids that is not apparent from feeding mode alone.

To determine the integration of locomotion and prey capture in divergent cottids, we examined feeding performance and kinematics of *B. cirrhosus* and compared this to the more generalized benthic *O. maculosus*, for which feeding mode and mouth morphology have been described (Norton, 1991). Although feeding morphology includes components of the hyoid, jaws and skull, mouth aperture size is an emergent property of these elements that is important when predicting behavior and performance (Wainwright et al., 2001; Higham et al., 2006b), and was used as a proxy of feeding morphology. We addressed the following questions in this study: (1) do the similarities in mouth morphology, despite differences in ecology, result in convergent feeding kinematics; and (2) are the patterns of integration between the locomotor and feeding systems comparable between *O. maculosus* and *B. cirrhosus*? We predicted that similar feeding morphology would result in similar feeding kinematics and feeding performance, and that *B. cirrhosus* would rely on suction to capture prey. We also predicted that the differences in ecology between *B. cirrhosus* and *O. maculosus* would result in differences in the integration of locomotion and feeding, indicating an overall disparity in feeding strategies. Alternatively, despite differences in ecology, *B. cirrhosus* and *O. maculosus* may exhibit similar integration of the locomotor and feeding systems, resulting in similar feeding strategies to capture prey.

MATERIALS AND METHODS

Experimental setup

Four *B. cirrhosus* (mean total length: 4.36±0.5 cm) and four *O. maculosus* (mean total length: 6.49±0.5 cm) specimens were seined from seagrass and algae beds off Ross Island (48°52.4′N, 125°09.5′W) and Wizard Island (48°51.5′N, 125°09.6′W) near the Bamfield Marine Sciences Centre (BMSC) in Bamfield, BC, Canada. Juvenile *B. cirrhosus* were chosen to match sizes of adult *O. maculosus*. In *Clinocottus analis*, ontogenetic changes in feeding kinematics do not occur after larvae settle from the plankton (Cook, 1996). Therefore, although *B. cirrhosus* were juveniles, ontogeny does not likely contribute to differences between this species and *O. maculosus*. After collection, specimens were housed in a flow-through sea table maintained at 10°C and were starved for 3 days prior to experiments. Specimens were collected under Fisheries and Oceans Canada license XR 80 2010 (T.E.H.), and all collection and experimental procedures were approved by the Animal Care Committee at BMSC.

To determine locomotor and feeding kinematics during prey capture, individuals were transferred to a filming tank (0.5×0.25×0.3 m, ~38 l), filled with the same flow-through seawater as the holding tank, and were acclimated for 10 min to 1 day, until they appeared calm and willing to feed. During filming, seawater flow was shut off to limit its influence on kinematics, and was re-started at the end of the filming trial to maintain water temperature and reduce animal stress. Individuals were filmed at 500 frames s^{-1} (1080×1080 pixels, Photron APX-RS, Photron USA, Inc., San Diego, CA, USA) from the lateral perspective (*B. cirrhosus* 36 trials, *O. maculosus* 23 trials). Gammarid amphipods were collected by hand from an intertidal region near BMSC and were used as prey items. Although these prey items have previously been considered non-evasive (Norton, 1995), they were capable of fast swimming speeds and escape responses. Thus, we consider them evasive with respect to other, non-evasive prey such as polychaete worms, bivalves, echinoderms and algae (Norton, 1995). Prey items were dropped into the tank once individuals appeared calm and were resting on the bottom of the tank (*B. cirrhosus* readily rested on the bottom in the absence of flow). Prey were not tethered, as is common in studies of aquatic prey capture. Prey items ranged in size from 3 to 8 mm and larger prey items were fed to larger individuals. Videos were included in the analysis when the predator was visible in lateral view, predator and prey were in focus, the entire length of the predator was visible to determine the initiation of a fast start and all kinematic landmarks were visible. Trials in which individuals fed from the bottom of the tank were included, as well as missed strikes. However, when a miss was followed by subsequent strikes, only the first strike was included. These criteria resulted in a total of 17 usable sequences for *B. cirrhosus* (four, three, six and three trials per individual) and 12 usable sequences for *O. maculosus* (two, three, two and five trials per individual).

Data analysis

Sequences were digitized in MATLAB (version R2009a, The MathWorks, Natick, MA, USA) using a custom program (Hedrick, 2008) from the initiation of a fast start toward the prey, which was readily apparent in both species after a pause when approaching the prey, until the mouth was closed and jaw protrusion returned to its resting state. Digitized points included: on the prey, (1) the point most distal from the predator, and on the predator, (2) the tip of the premaxilla, (3) the tip of the mandible, (4) the eye and (5) the distal margin of the caudal fin at the midline (Fig. 1A). Coordinates were imported into Microsoft Excel 2008 (Microsoft Corporation, Redmond, WA, USA) for further calculations, including: predator total length (TL; linear distance from the tip of the premaxilla to the distal margin of the caudal fin), predator–prey distance (PPD; linear distance from the tip of the premaxilla to the prey) at the start

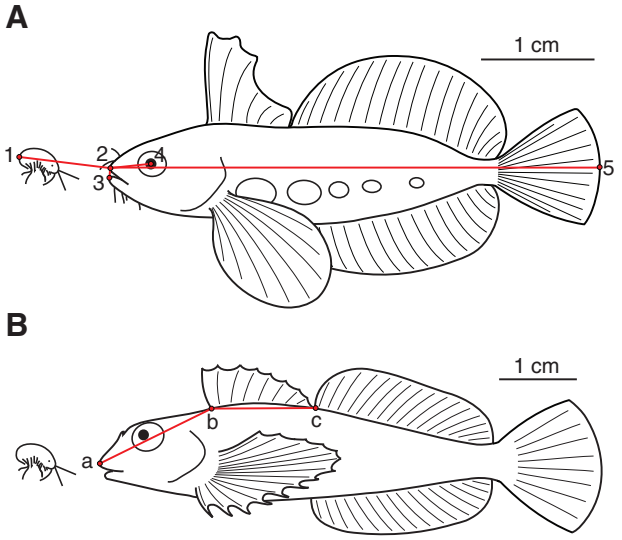

Fig. 1. Representative diagrams of (A) digitized anatomical landmarks and kinematic measurements shown on *Blepsias cirrhosus* and (B) static measurements shown on *Oligocottus maculosus*. All measurements were taken from each species. Diagrams are scaled to the same total length to show relative differences in body morphology between species. Kinematic landmarks (shown in A) were used to calculate predator total length (points 2 to 5), predator–prey distance (points 1 to 2), gape (points 2 to 3) and upper jaw protrusion (points 2 to 4). Cranial elevation (angle abc, shown in B) was calculated as the difference between values at the start and the maximum. See Materials and methods for a description of additional calculated variables.

and at mouth opening, predator velocity (linear displacement of the eye over time, smoothed using a quintic spline in MATLAB) at the maximum and at peak gape, peak predator acceleration and deceleration (predator velocity displacement over time), peak prey velocity (linear displacement of the prey over time), peak gape (the maximum linear distance between the tips of the premaxilla and mandible), and peak jaw protrusion (the maximum linear distance from the tip of the premaxilla to the eye). Peak cranial elevation (displacement of the angle formed by the tip of the premaxilla and the bases of the first spine of the first and second dorsal fins; Fig. 1B) was calculated in ImageJ (version 1.43r, NIH, Bethesda, MD, USA) at the frames of fast-start initiation and maximal displacement (determined visually). Finally, timing of all kinematic events was recorded, in addition to time of fin abduction, time of mouth opening, time of prey capture (when the prey crossed the boundary created by the tips of the premaxilla and the mandible), time to peak gape (TTPG; duration from mouth opening to peak gape) and total duration (from fast start initiation to peak gape). Timing (except for total duration) was normalized to ms before or after peak gape, with events occurring before peak gape having negative values. To determine whether species displayed similar mouth sizes and, therefore, feeding morphology, mouth area was calculated by assuming a circular aperture shape at peak gape, where peak gape distance represents the diameter.

Statistical analysis

Statistics were performed in JMP (version 8.0.2, SAS Institute Inc., Cary, NC, USA). Mouth area was log-transformed and regressed against log-transformed total length, similar to Norton (Norton, 1991). A regression line was fit to the combined data for both species. Each species was then constrained to the combined regression equation, and significance of the fit was determined. For the remaining analyses, length measurements (PPD, peak gape, jaw protrusion), velocities (predator and prey) and accelerations were scaled to TL, although data reported below are unscaled values.

Only *B. cirrhosus* had enough missed strikes (six out of 17 usable sequences, one to two misses per individual) to determine kinematic differences between successful and unsuccessful strikes. Missed strikes were not significantly different than captured strikes for individual means of all variables (*t*-tests, $P>0.2131$). Similarly, only *B. cirrhosus* captured prey from the bottom (five out of 17 sequences, zero to three bottom strikes per individual). However, strikes near the bottom occurred during forward movement (and were not directed at the bottom) and individual means were not significantly different from strikes in the water column (*t*-tests, $P>0.1129$), except for PPD at mouth opening (*t*-test, $P=0.0157$). Therefore, data were pooled for further analyses.

To distinguish differences between species, all dependent variables were assessed using two-way ANOVAs with species (fixed factor) and individual (random factor nested within species) as independent variables. Results were Bonferroni corrected (Rice, 1989) and resulting critical values were $P<0.004$ for kinematic and $P<0.005$ for timing variables. Sequential Bonferroni corrections were not used because these are more conservative and can inflate Type II error (Moran, 2003). Additionally, the coefficient of variation (c.v.) for all variables was calculated for all individuals, and significance was tested using a *t*-test on species to determine differences in stereotypy (Wainwright et al., 2008). Results were also Bonferroni corrected using the same critical values. Finally, Pearson correlations were used to indicate locomotor variables that were correlated with feeding kinematics to determine the integration between locomotion and feeding.

To explore the variability of and visually summarize feeding and locomotor kinematics, a principal components analysis (PCA) was run using the correlation matrix on the mean of all kinematic variables for each individual. This was done to maintain the assumption of independent samples. Variables were correlated to the PC scores for each PC axis and significance was determined using a Pearson correlation. A *t*-test on PC scores was used to determine whether species differed significantly in placement along each PC axis.

RESULTS

Both *B. cirrhosus* and *O. maculosus* captured amphipod prey in the water column using a fast start to approach the prey and then a combination of suction and ram for capture. Individuals oriented to the prey, sometimes approaching with short bursts of swimming, and paused before beginning the fast start. Strikes were initiated from ~1.8 and 2.6 cm away from the prey for *B. cirrhosus* and *O. maculosus*, respectively, which was 0.41 TL for both species. Both species rested on the bottom of the tank and entered the water column to capture swimming prey; however, *B. cirrhosus* readily captured prey from any depth (including the bottom of the tank) whereas *O. maculosus* always captured prey almost immediately after being introduced at the top of the water column, and rapidly returned to the bottom of the tank. Capture success was greater for *O. maculosus* (91% in 23 trials) than *B. cirrhosus* (72% in 36 trials).

Feeding morphology (mouth size) and kinematics were similar between species. The relationship between mouth area and total length shows that both species have similar mouth areas for their given sizes (Fig. 2). Species were constrained to a common regression line ($y=1.28x-0.80$), which was significant for both species (*B. cirrhosus*, $t=58.2$, $P<0.0001$; *O. maculosus*, $t=56.95$,

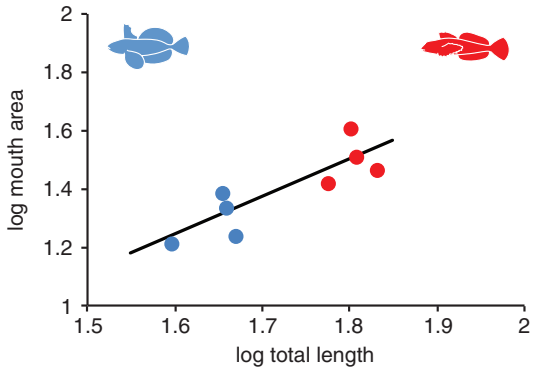

Fig. 2. Relationship between log-transformed mouth area (mm^2) and log-transformed total length (mm) for *B. cirrhosus* (blue) and *O. maculosus* (red). Mouth area was calculated by assuming that peak gape represents the diameter of a circle. Both species fall on a common regression line (y=1.28x–0.80), indicating that both should employ similar suction-feeding strategies to capture prey (Norton, 1991).

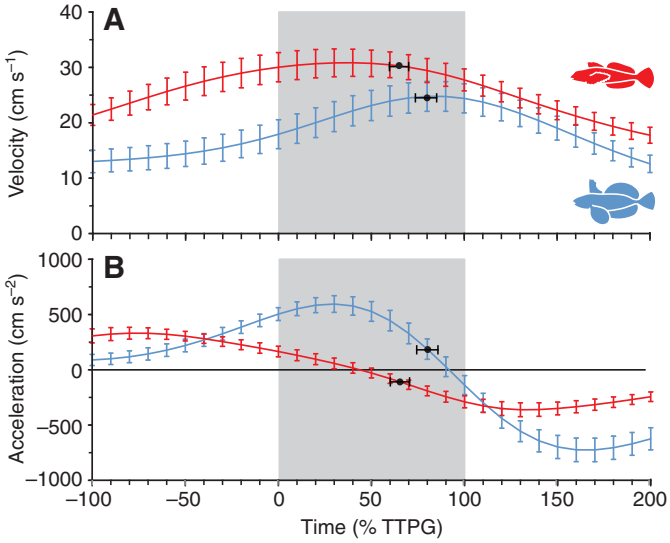

Fig. 3. (A) Velocity and (B) acceleration of *B. cirrhosus* (blue) and *O. maculosus* (red) while feeding on amphipod prey (data are means ± s.e.m.). Timing was scaled to time to peak gape (% TTPG) and trials were interpolated to 31 points from 100% TTPG before mouth opening to 100% TTPG after peak gape. Gray shading represents TTPG, bounded by time of mouth opening and peak gape. Black circles on each trace indicate mean ± s.e.m. time of prey capture for each species. Although *B. cirrhosus* relies on rapid acceleration to increase velocity and capture prey near peak gape, *O. maculosus* accelerates more slowly before mouth opening and decelerates as the prey is captured.

P<0.0001). Elevation of the cranium was 18.9±2.33 and 13.3±1.19 deg for *B. cirrhosus* and *O. maculosus*, respectively. Additionally, the jaws were protruded to ~3% TL in both species. Although peak gape appeared smaller for *B. cirrhosus* (*B. cirrhosus*, 0.49±0.02 cm; *O. maculosus*, 0.63±0.03 cm), differences in cranial elevation, protrusion and gape were not significant (ANOVAs, P>0.01).

Univariate tests on each variable showed that both species relied on degrees of ram and suction during prey capture that resulted in overall similar feeding modes. Peak velocity (*B. cirrhosus*, 25.5±2.67 cm s^{-1}; *O. maculosus*, 30.3±2.74 cm s^{-1}) and velocity at peak gape (*B. cirrhosus*, 24.4±2.63 cm s^{-1}; *O. maculosus*, 26.4±2.28 cm s^{-1}) were comparable between the two species. *Blepsias cirrhosus* and *O. maculosus* also initiated mouth opening at 0.77±0.09 and 1.27±0.16 cm from the prey, respectively. Peak prey velocities were 67.4±15.2 and 93.2±10.7 cm s^{-1} for *B. cirrhosus* and *O. maculosus*, respectively. None of these variables were significantly different between species (ANOVAs, P>0.008; Table 1). Although time of prey capture indicated that *B. cirrhosus* captured prey later in the gape cycle, and closer to peak gape, than *O. maculosus* (Table 1), when this value was scaled to a percentage of TTPG, no significant differences were found (ANOVA, P=0.10).

Maximum body acceleration in *B. cirrhosus* occurs during mouth opening, and forward velocity was maintained throughout prey capture, with deceleration beginning prior to the time of peak gape (Fig. 3A). In contrast, *O. maculosus* accelerated before mouth opening, slowing velocity and beginning deceleration prior to the time of prey capture (Fig. 3B). Both species continued deceleration

Table 1. Means ± s.e.m. of select kinematic variables after standardization to total length

Variable	*Blepsias cirrhosus* (N=17)	*Oligocottus maculosus* (N=12)	Species	Individual
Total length (cm)	4.36±0.11	6.49±0.13	0.000*	0.003*
Peak velocity (BL s^{-1})	5.91±0.63	4.67±0.41	0.049	0.007
Time of peak velocity, normalized (ms)	–3.76±1.55	–19.00±4.65	0.000*	0.000*
Peak acceleration (BL s^{-2})	155.61±18.32	63.85±6.32	0.000*	0.281
Time of peak acceleration, normalized (ms)	–16.12±2.19	–56.17±6.86	0.000*	0.004*
Peak deceleration (BL s^{-2})	–190.76±23.56	–61.74±7.02	0.000*	0.011
Time of peak deceleration, normalized (ms)	12.59±1.61	11.50±3.82	0.934	0.655
Peak prey velocity (captures; BL s^{-1})	20.27±4.32	15.55±1.34	0.240	0.285
Time of peak prey velocity, normalized (ms)	0.55±1.40	–3.45±2.07	0.059	0.002*
Time of mouth opening, normalized (ms)	–19.65±1.89	–31.83±2.32	0.000*	0.002*
PPD opening/TL	0.18±0.02	0.20±0.03	0.192	0.093
Time of prey capture, normalized (ms)	–4.00±1.13	–10.36±1.76	0.001*	0.056
Peak gape/TL	0.11±0.00	0.10±0.00	0.012	0.077
Time to peak gape (ms)	19.65±1.89	31.83±2.32	0.000*	0.002*
Velocity at peak gape (BL s^{-1})	5.64±0.61	4.05±0.33	0.008	0.011
Total duration (ms)	128.82±17.15	98.83±10.63	0.044	0.000*

N, number of trials.
P-values from two-way ANOVA are shown for species and individual effects.
*Significant differences at P<0.004 (kinematic variables) or P<0.005 (timing variables).

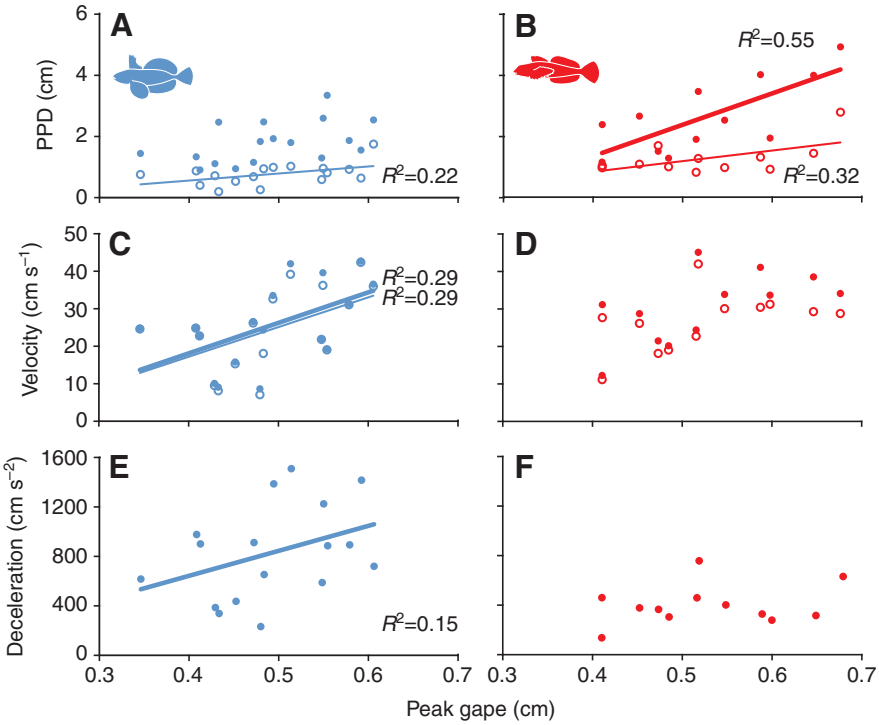

Fig. 4. Integration of locomotor variables with peak gape for *B. cirrhosus* (blue) and *O. maculosus* (red). Points are shown on unstandarized scales for each trial for both species, but only significant correlations from standardized (to total length) data are indicated. Regression lines and associated R^2-values are shown for unstandardized data. (A,B) Predator–prey distance (PPD) at the start (solid circles and thick line) and at mouth opening (open circles and thin lines); (C,D) peak velocity (solid circles and thick line) and velocity at peak gape (open circles and thin line); and (E,F) absolute value of peak deceleration. PPD, strike velocity and deceleration are correlated to peak gape in *B. cirrhosus*, whereas only PPD is correlated to peak gape in *O. maculosus*, indicating a greater contribution of the locomotor system to the feeding strategy of *B. cirrhosus*.

until a peak after the time of peak gape. Although peak body velocity was not significantly different between species, it occurred less than 4 ms before peak gape in *B. cirrhosus*, but 19 ms before peak gape in *O. maculosus* (ANOVA, P=0.049; Table 1). Additionally, peak body acceleration was significantly greater for *B. cirrhosus* (675.1±75.8 cm s^{-2}; Fig. 3B) than for *O. maculosus* (416.3±43.2 cm s^{-2}; ANOVA, P<0.001). However, both species reach peak deceleration ~12 ms after peak gape, aided by pectoral fin protraction, with maximum pectoral fin abduction occurring more than 30 ms after peak gape. Feeding and locomotor kinematics were highly variable for both species, and both species exhibited comparable levels of stereotypy (measured using c.v.; *t*-tests, P>0.05).

As indicated by correlations between locomotor and feeding variables, integration between locomotion and feeding was more apparent in *B. cirrhosus* than *O. maculosus*. For *B. cirrhosus*, PPD at mouth opening (Fig. 4A), approach velocity (Fig. 4C) and absolute value of deceleration (Fig. 4E) were positively correlated with peak gape (Pearson correlations, r>0.52, P<0.03). For *O. maculosus*, PPD at the start and at mouth opening were the only variables correlated with peak gape (Pearson correlations, r=0.60, P=0.04; Fig. 4B). Integration was not observed between predator approach velocity (Fig. 4D) or predator deceleration (Fig. 4F) in *O. maculosus*.

Species were distinct in multivariate space, and were separated by two axes of variation (Fig. 5) that explained 60.7% of the total variance between species (PC1 32.8%, PC2 27.9%). PC1 was positively correlated with peak acceleration, time of peak acceleration, time of peak velocity, time of mouth opening, time of prey capture and peak deceleration (Pearson correlations, r>0.72, P<0.044; Table 2) and was negatively correlated with TTPG (Pearson correlation, r=–0.93, P=0.0009; Table 2). This axis represents differences in magnitude of acceleration and deceleration, and the timing of locomotor and feeding performance measures (occurrence prior to or near the time of peak gape). PC2 was positively correlated with many of the remaining variables, including starting PPD, peak velocity, peak gape, velocity at peak gape and peak cranial elevation (Pearson correlations, r>0.74, P<0.036; Table 2). These variables summarize differences in feeding mode; therefore, PC2 represents an axis describing degrees of ram and suction use. *Blepsias cirrhosus* and *O. maculosus* differed significantly in their placement along PC1 (integration, *t*-test, t=–3.81, P=0.01) but not PC2 (feeding mode, *t*-test, t=–0.47, P=0.66).

DISCUSSION

Morphological variation is often the basis for studies addressing the link between form and function. However, morphology does not always provide a direct link to function, as structures can perform multiple functions and, in some cases, structures that appear different can accomplish similar functions (Wainwright, 2007). Our study focused on two cottid species that exhibit comparable feeding

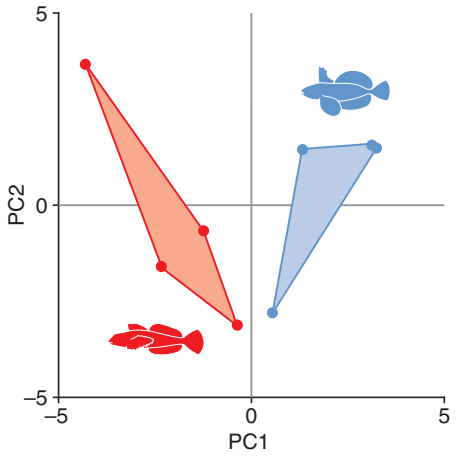

Fig. 5. Principal component (PC) scores for individuals of *B. cirrhosus* (blue) and *O. maculosus* (red) plotted in PC space. For kinematic variables that correlated with each axis, see Table 2. Species separate primarily along the PC1 axis.

Table 2. Variable correlations with principal component axes

Variable	PC1	PC2
PPD at start	–0.37	0.81*
Peak acceleration	0.79*	0.55
Time of peak acceleration	0.92*	–0.23
Peak velocity	0.40	0.88*
Time of peak velocity	0.80*	–0.58
PPD at mouth opening	–0.34	0.23
Time of mouth opening	0.93*	–0.20
Peak prey velocity	0.31	–0.18
Time of peak prey velocity	0.50	–0.54
Time of prey capture	0.72*	–0.31
Peak gape	0.37	0.74*
Velocity at peak gape	0.61	0.74*
Time to peak gape	–0.93*	0.20
Peak cranial elevation	0.38	0.74*
Time of max cranial elevation	0.28	–0.16
Peak protrusion	0.21	0.40
Time of max fin abduction	0.37	–0.27
Peak deceleration	0.88*	0.43
Time of peak deceleration	0.21	–0.50
Total duration	–0.18	0.00

*Significant correlations at $P<0.05$; Pearson correlation between original variables and principal component scores for axes 1 (PC1) and 2 (PC2).
PPD, predator–prey distance.

morphology (mouth size) and kinematics, but exhibit variation in locomotor performance, locomotor integration with feeding and, therefore, feeding strategy. For both *B. cirrhosus* and *O. maculosus*, mouth size predicts feeding kinematics involving suction. However, *B. cirrhosus* achieved greater acceleration during prey capture and displayed a tighter integration of locomotor and feeding variables. Our prediction that the feeding strategy of divergent suction-feeding cottids would be reflected in levels of integration of locomotion and feeding is supported. However, locomotor morphology was not quantified in this study, and it is possible that differences in locomotor kinematics and performance during prey capture result from differences in locomotor morphology, an area that remains to be explored.

This is the first study to address the integration of locomotion and feeding in cottids, which are BCF transient locomotor specialists (Webb, 1984b). Studies of locomotion and feeding in BCF specialists have not addressed the integration of these behaviors, and have not included predator velocity and acceleration profiles when determining differences between species (Webb and Skadsen, 1980; Rand and Lauder, 1981; Webb, 1984a; Harper and Blake, 1991; Porter and Motta, 2004). Our study indicates that multidimensional analyses of locomotor and feeding performance can provide insight into differences between species that are not apparent otherwise. Therefore, future studies that aim to explain patterns of feeding and locomotor diversity in fishes should include acceleration profiles that not only describe the magnitude of velocity and acceleration, but also how these variables change with time and how they are related to the timing of other variables, such as prey capture. This type of analysis has been valuable in inferring patterns of diversity in divergent marine cottids with similar feeding morphology and kinematics.

Use of suction during prey capture

Sculpins in this study displayed a similar mouth size, consistent with previous descriptions of suction-feeding cottids. For several species of cottids, Norton (Norton, 1991) determined that the relationship between mouth area and body length could accurately predict feeding mode. Differences in mouth area were used as a proxy of overall morphological feeding differences, and primarily separated species into large-mouthed ram feeders and small-mouthed suction feeders [fig. 1 in Norton (Norton, 1991)]. When *B. cirrhosus* and *O. maculosus* are plotted in a similar manner (Fig. 2), both species fall on the same regression line. In morphological space, these species occur in the same area occupied by other small-mouthed cottids from Norton (Norton, 1991), including *O. maculosus*. Therefore, both species in this study exhibit similar mouth morphology (mouth size) that is consistent with the ability for suction feeding during prey capture.

Similarities in prey velocity during prey capture indicated not only that predator strategies were not affected by prey movement, but also that suction performance was similar between species. However, suction performance may have been greater in *O. maculosus* than in *B. cirrhosus*. Suction performance can be estimated by prey velocity at prey capture, and in this study, *O. maculosus* was able to ingest prey at a greater velocity than *B. cirrhosus*, although this difference was not significant. It is possible that differences in suction generation performance, parameters that were not quantified in this study (fluid flow velocity, suction force, etc.), could have contributed to increased suction performance in *O. maculosus*. For example, it is not known whether peak fluid speed occurs at the time of peak gape, as is the case for other teleosts (Day et al., 2005; Higham et al., 2006a). Future work utilizing digital particle image velocimetry to assess the hydrodynamics of suction feeding in cottids will allow a more accurate interpretation of the patterns of prey capture behavior observed in this study.

Locomotor and feeding strategies

Differences in fast-start performance during prey capture between *B. cirrhosus* and *O. maculosus* are associated with differences in microhabitat (benthic *vs* pelagic). The similarity in results from both univariate analyses and the PCA indicates that the feeding strategies of each species are prominent and defining. Whereas *O. maculosus* adopts a strategy of early acceleration, reaching peak velocity and beginning to decelerate as the prey is captured, *B. cirrhosus* accelerates just prior to prey capture, resulting in peak velocity occurring at or just after prey capture and deceleration beginning at peak gape (Fig. 3). This strategy of *B. cirrhosus* is similar to that of *Micropterus salmoides* and *Lepomis macrochirus*, which both accelerate prior to peak gape and throughout prey capture (Higham, 2007b). The alternative strategy of *O. maculosus* may be due to its benthic behavior compared with the pelagic behavior of the other species. *Oligocottus maculosus* typically turns around after prey capture to immediately return to the bottom of the aquarium. Therefore, deceleration through prey capture may facilitate turning maneuverability and escape to the protection of rocks and vegetation after prey capture. In shallow tidepool habitats, *O. maculosus* are best protected from predators when sitting still on the benthos among vegetation. Therefore, this species likely relies on a strategy that minimizes exposure to predators. Pelagic species, such as *B. cirrhosus*, *M. salmoides* and *L. macrochirus* do not have this constraint, and therefore display a feeding strategy that allows them to overrun prey while remaining in the water column.

These differences in feeding strategies between species might be responsible for the greater capture success rates observed in *O. maculosus* compared with *B. cirrhosus*. Differences in acceleration profiles reflect differences in predator velocity at prey capture such that velocity is increasing for *B. cirrhosus* but decreasing for *O. maculosus* as the prey enters the mouth. Therefore, *O. maculosus*

is likely better able to aim at prey because accuracy increases with decreased velocity (Higham et al., 2006b). In the present study, missed strikes qualitatively appeared to be the result of poor aim and not prey behavior, as prey escape responses were typically initiated after a failed strike. Therefore, increased accuracy in *O. maculosus* likely results in greater capture success.

The feeding strategies of cottids in this study differed primarily in the reliance on integration. Compared with *O. maculosus*, *B. cirrhosus* exhibited a greater degree of integration between the locomotor and feeding systems during prey capture (Fig. 4). However, this does not rule out the possibility that benthic station-holding *O. maculosus* also rely on some degree of integration of the locomotor system with feeding. For example, similar velocities were used by both species to approach the prey and both species employed pectoral fin protraction to decelerate after prey capture. Future work investigating the detailed kinematics of the locomotor system during prey capture might reveal a level of integration not found in the present study.

Both species of cottids in this study relied on fast starts to capture prey. This behavior is well documented in several cottids (Norton, 1991; Cook, 1996) and esocid pikes (Webb and Skadsen, 1980; Rand and Lauder, 1981; Harper and Blake, 1991), and supports the hypothesis that the sculpin and pike body forms are used to generate rapid acceleration during prey capture as a means to ambush prey (Webb, 1984b). However, cottid adaptations for BCF transient propulsion are drag minimizing, unlike the thrust-maximizing body form of esocids (Webb, 1984b), and this is reflected by greater velocities and accelerations during prey captures and escapes in esocids. During feeding fast starts, *Esox lucius* accelerates between 174 and 344 body lengths (BL) s^{-2}, and reaches velocities of 8.5 BL s^{-1} (Harper and Blake, 1991). In contrast, cottids in the present study performed similar to the cottid *Myoxocephalus scorpius*, which lunged at prey with a velocity of ~5 BL s^{-1} and accelerated at only 91 BL s^{-2} (Beddow et al., 1995). Although cottid feeding fast-start performance differs from that of esocids in magnitude, *B. cirrhosus* utilizes ~63% of maximal escape performance during feeding strikes (S. Kawano, personal communication), which is similar to the esocid *E. lucius*, which reaches ~66% of maximal escape performance (Harper and Blake, 1991). The ability of *B. cirrhosus* to closely match feeding and escape performance, similar to esocids, indicates that the feeding strategy is similar between taxa even though the magnitude of performance is lower. Alternatively, *M. scorpius* utilizes 54% of maximal performance during feeding strikes (James and Johnston, 1998; Temple and Johnston, 1998). Given the differences previously described between *B. cirrhosus* and *O. maculosus*, as well as the similarity in benthic ecology and body form of *O. maculosus* and *M. scorpius*, it can be predicted that *O. maculosus* might rely on a feeding strategy similar to that of *M. scorpius*, where a lesser degree of maximal escape performance is utilized during feeding fast starts. However, this hypothesis has not yet been tested.

Implications for diversity

Freshwater cottids can display variation in morphology based on habitat, resulting in forms more or less morphologically adapted for benthic station holding (Kerfoot and Schaefer, 2006). Our study provides evidence that variation in ecology can contribute to variation in locomotor performance that is then reflected in the integration of locomotion and feeding, and overall feeding strategy. This relationship between ecology and function is likely linked by a relationship to morphology. For example, *O. maculosus* pectoral fins are specialized for benthic station holding (Gosline, 1994), and a trade-off in pectoral fin function and performance might limit the movements of the pectoral fins across behaviors. Specifically, the stabilizing actions of the pectoral fins during swimming behaviors could be compromised, resulting in their observed increased reliance on deceleration at prey capture to moderate this constraint. Alternatively, *B. cirrhosus* pectoral fins are released from the morphological constraints of station holding, allowing the fins to evolve further integration of locomotion and feeding, as was observed in this study. Further analyses of the effects of habitat on morphology and function in cottids would give a better indication of whether these functional trade-offs are generally apparent across cottids or are specific to the two species studied here.

Recent studies have supported the idea that deep subtidal cottids like *B. cirrhosus* represent an ancestral form whereas cottids in shallower or freshwater habitats like *O. maculosus* represent more derived forms (Ramon and Knope, 2008; Mandic et al., 2009). If the active, pelagic lifestyle of *B. cirrhosus* (Marliave, 1975) is representative of ancestral cottids, it is possible that swimming performance has been ancestrally selected for, facilitating integration during prey capture in more basal species. In cichlids, ram speed and peak gape are evolutionarily correlated (Higham et al., 2007). However, this relationship was only observed for *B. cirrhosus* in this study. The lack of a relationship in the more derived *O. maculosus* indicates that ram speed may not be evolutionarily correlated to peak gape in cottids, and that integration between locomotion and feeding has been lost in more derived lineages. It is possible that, in derived shallow-water forms, the need for integration is superseded by demands from the habitat. This is likely a common pattern among vertebrates, but one that is apparent in cottids because of their specialized benthic ecology. These hypotheses should be tested within a phylogenetic framework to determine how changes in habitat, morphology and performance are correlated in cottids.

ACKNOWLEDGEMENTS

B. Rogers and D. Riddell from the Bamfield Marine Sciences Centre provided facilities and helped with setup and materials. Fish were collected in conjunction with the Icthyology and Biomechanics field courses at BMSC. Additional assistance in the field was provided by K. Foster and S. Kawano. B. Brown provided guidance for statistical analyses and two anonymous reviewers provided insightful comments on the manuscript. Funding was provided by an R. C. Edwards Fellowship from Clemson University to E.A.K. and startup funds to T.E.H.

REFERENCES

Alfaro, M. E. (2003). Sweeping and striking: a kinematic study of the trunk during prey capture in three thamnophiine snakes. *J. Exp. Biol.* **206**, 2381-2392.
Beddow, T. A., Van Leeuwen, J. L. and Johnston, I. A. (1995). Swimming kinematics of fast starts are altered by temperature acclimation in the marine fish *Myoxocephalus scorpius*. *J. Exp. Biol.* **198**, 203-208.
Bellwood, D. R. and Choat, J. H. (1990). A functional analysis of grazing in parrotfishes (Family Scaridae) – the ecological implications. *Environ. Biol. Fishes* **28**, 189-214.
Collar, D. C., Wainwright, P. C. and Alfaro, M. E. (2008). Integrated diversification of locomotion and feeding in labrid fishes. *Biol. Lett.* **4**, 84-86.
Cook, A. (1996). Ontogeny of feeding morphology and kinematics in juvenile fishes: a case study of the cottid fish *Clinocottus analis*. *J. Exp. Biol.* **199**, 1961-1971.
Day, S. W., Higham, T. E., Cheer, A. Y. and Wainwright, P. C. (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**, 2661-2671.
Dean, M. N. (2003). Suction feeding in the pipid frog, *Hymenochirus boettgeri*: kinematic and behavioral considerations. *Copeia* **2003**, 879-886.
Dunbar, D. C. and Badam, G. L. (2000). Locomotion and posture during terminal branch feeding. *Int. J. Primatol.* **21**, 649-669.
Geerlink, P. J. (1987). The role of the pectoral fins in the braking of makerel, cod, and saithe. *Neth. J. Zool.* **37**, 81-104.
Gerstner, C. L. (1999). Maneuverability of four species of coral-reef fish that differ in body and pectoral fin morphology. *Can. J. Zool.* **77**, 1102-1110.
Goldbogen, J. A., Pyenson, N. D. and Shadwick, R. E. (2007). Big gulps require high drag for fin whale lunge feeding. *Mar. Ecol. Prog. Ser.* **349**, 289-301.
Gosline, W. A. (1994). Function and structure in the paired fins of scorpaeniform fishes. *Environ. Biol. Fishes* **40**, 219-226.

Gray, L. A. and Nishikawa, K. C. (1995). Feeding kinematics of phyllomedusine tree frogs. *J. Exp. Biol.* **198**, 457-463.
Harper, D. G. and Blake, R. W. (1991). Prey capture and the fast-start performance of northern pike *Esox lucius*. *J. Exp. Biol.* **155**, 175-192.
Hedrick, T. L. (2008). Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspiration Biomimetics* **3**, 034001.
Higham, T. E. (2007a). The integration of locomotion and prey capture in vertebrates: morphology, behavior, and performance. *Integr. Comp. Biol.* **47**, 82-95.
Higham, T. E. (2007b). Feeding, fins and braking maneuvers: locomotion during prey capture in centrarchid fishes. *J. Exp. Biol.* **210**, 107-117.
Higham, T. E., Day, S. W. and Wainwright, P. C. (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**, 2653-2660.
Higham, T. E., Day, S. W. and Wainwright, P. C. (2006a). The pressures of suction feeding: the relation between buccal pressure and induced fluid speed in centrarchid fishes. *J. Exp. Biol.* **209**, 3281-3287.
Higham, T. E., Day, S. W. and Wainwright, P. C. (2006b). Multidimensional analysis of suction feeding performance in fishes: fluid speed, acceleration, strike accuracy and the ingested volume of water. *J. Exp. Biol.* **209**, 2713-2725.
Higham, T. E., Hulsey, C. D., Rican, O. and Carroll, A. M. (2007). Feeding with speed: prey capture evolution in cichilds. *J. Evol. Biol.* **20**, 70-78.
Hoff, K. S., Lannoo, M. J. and Wassersug, R. J. (1985). Kinematics of midwater prey capture by ambystoma (Caudata: Ambystomatidae) larvae. *Copeia* **1985**, 247-251.
Irschick, D. J. and Losos, J. B. (1998). A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* **52**, 219-226.
Jaenicke, H. W., Celewycz, A. G., Bailey, J. E. and Orsi, J. I. (1985). Paired open beach seines to study estuarine migrations of juvenile salmon. *Mar. Fish. Rev.* **46**, 62-67.
James, R. S. and Johnston, I. A. (1998). Scaling of muscle performance during escape responses in the fish *Myoxocephalus scorpius* L. *J. Exp. Biol.* **201**, 913-923.
Kane, E. A. and Marshall, C. D. (2009). Comparative feeding kinematics and performance of odontocetes: belugas, Pacific white-sided dolphins, and long-finned pilot whales. *J. Exp. Biol.* **212**, 3939-3950.
Kerfoot, J. R. and Schaefer, J. F. (2006). Ecomorphology and habitat utilization of *Cottus* species. *Environ. Biol. Fishes* **76**, 1-13.
Kolpakov, N. V. and Dolganova, N. T. (2006). On the biology of *Blepsias cirrhosus* (Hemitripteridae) from coastal waters of northern Primorye. *J. Ichthyol.* **46**, 454-459.
Lauder, G. V. (1985). Aquatic feeding in lower vertebrates. In *Functional Vertebrate Morphology* (eds. M. Hildebrand D. M. Bramble K. F. Liem and D. B. Wake), pp. 210-229. Cambridge, MA: Harvard University Press.
Liem, K. F. (1980). Adaptive significance of intraspecific and interspecific differences in the feeding repertoires of cichlid fishes. *Am. Zool.* **20**, 295-314.
Mandic, M., Todgham, A. E. and Richards, J. G. (2009). Mechanisms and evolution of hypoxia tolerance in fish. *Proc. R. Soc. Lond. B Biol. Sci.* **276**, 735-744.
Marliave, J. B. (1975). The behavioral transformation from the planktonic larval stage of some marine fishes reared in the lab. PhD dissertation, University of British Columbia.
Montuelle, S. J., Herrel, A., Libourel, P. A., Reveret, L. and Bels, V. L. (2009). Locomotor-feeding coupling during prey capture in a lizard (*Gerrhosaurus major*): effects of prehension mode. *J. Exp. Biol.* **212**, 768-777.
Moran, M. D. (2003). Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* **100**, 403-405.
Muller, M. and Osse, J. W. M. (1984). Hydrodynamics of suction feeding in fish. *Trans. Zool. Soc. Lond.* **37**, 51-135.
Muller, M., Osse, J. W. M. and Verhagen, J. H. G. (1982). A quantitative hydrodynamic model of suction feeding in fish. *J. Theor. Biol.* **95**, 49–79.
Nakamura, R. (1971). Food of two cohabiting tide-pool Cottidae. *J. Fish. Res. Board Can.* **28**, 928-932.
Nemeth, D. H. (1997). Modulation of attack behavior and its effect on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. *J. Exp. Biol.* **200**, 2155-2164.
Norton, S. F. (1991). Capture success and diet of cottid fishes – the role of predator morphology and attack kinematics. *Ecology* **72**, 1807-1819.
Norton, S. F. (1995). A functional approach to ecomorphological patterns of feeding in cottid fishes. *Environ. Biol. Fishes* **44**, 61-78.
Norton, S. F. and Brainerd, E. L. (1993). Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. Exp. Biol.* **176**, 11-29.
Nyberg, D. W. (1971). Prey capture in the largemouth bass. *Am. Midl. Nat.* **86**, 128-144.
Porter, H. T. and Motta, P. J. (2004). A comparison of strike and prey capture kinematics of three species of piscivorous fishes: Florida gar (*Lepisosteus platyrhincus*), redfin needlefish (*Strongylura notata*), and great barracuda (*Sphyraena barracuda*). *Mar. Biol.* **145**, 989-1000.
Ramon, M. L. and Knope, M. L. (2008). Molecular support for marine sculpin (Cottidae; Oligocottinae) diversification during the transition from the subtidal to intertidal habitat in the Northeastern Pacific Ocean. *Mol. Phylogenet. Evol.* **48**, 475-483.
Rand, D. M. and Lauder, G. V. (1981). Prey capture in the chain pickerel, *Esox niger*: correlations between feeding and locomotor behavior. *Can. J. Zool.* **59**, 1072-1078.
Rice, A. N. (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**, 255-267.
Rice, A. N. and Westneat, M. W. (2005). Coordination of feeding, locomotor and visual systems in parrottishes (Teleostei: Labridae). *J. Exp. Biol.* **208**, 3503-3518.
Rice, A. N., Cooper, W. J. and Westneat, M. W. (2008). Diversification of coordination patterns during feeding behaviour in cheiline wrasses. *Biol. J. Linn. Soc.* **93**, 289-308.
Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223-225.
Shifferman, E. and Eilam, D. (2004). Movement and direction of movement of a simulated prey affect the success rate in barm owl *Tyto alba* attack. *J. Avian Biol.* **35**, 111-116.
Strauss, R. E. and Fuiman, L. A. (1985). Quantitative comparisons of body form and allometry in larval and adult Pacific sculpins (Teleostei: Cottidae). *Can. J. Zool.* **63**, 1582-1589.
Svanback, R., Wainwright, P. C. and Ferry-Graham, L. A. (2002). Linking cranial kinematics, buccal pressure, and suction feeding performance in largemouth bass. *Physiol. Biochem. Zool.* **75**, 532-543.
Temple, G. K. and Johnston, I. A. (1998). Testing hypotheses concerning the phenotypic plasticity of escape performance in fish of the family Cottidae. *J. Exp. Biol.* **201**, 317-331.
Wainwright, P. C. (2007). Functional versus morphological diversity in macroevolution. *Annu. Rev. Ecol. Evol. Syst.* **38**, 381-401.
Wainwright, P. C., Ferry-Graham, L. A., Waltzek, T. B., Carroll, A. M., Hulsey, C. D. and Grubich, J. R. (2001). Evaluating the use of ram and suction during prey capture by cichlid fishes. *J. Exp. Biol.* **204**, 3039-3051.
Wainwright, P. C., Mehta, R. S. and Higham, T. E. (2008). Stereotypy, flexibility and coordination: key concepts in behavioral functional morphology. *J. Exp. Biol.* **211**, 3523-3528.
Webb, P. W. (1984a). Body and fin form and strike tactics of four teleost predators attacking fathead minnow (*Pimephales promelas*) prey. *Can. J. Fish. Aquat. Sci.* **41**, 157-165.
Webb, P. W. (1984b). Body form, locomotion, and foraging in aquatic vertebrates. *Am. Zool.* **24**, 107-120.
Webb, P. W. and Skadsen, J. M. (1980). Strike tactics of *Esox*. *Can. J. Zool.* **58**, 1462-1469.
Webb, P. W., Gerstner, C. L. and Minton, S. T. (1996). Station-holding by the mottled sculpin, *Cottus bairdi* (Teleostei: Cottidae), and other fishes. *Copeia* **1996**, 488-493.
Yoshiyama, R. M. (1980). Food habits of three species of rocky intertidal sculpins (Cottidae) in central California. *Copeia* **1980**, 515-525.