

Coordination of feeding, locomotor and visual systems in parrotfishes (Teleostei: Labridae)

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Summary

Fishes require complex coordinated motions of the jaws, body and fins during feeding in order to successfully execute the strike or bite and then move away from the predation site. In conjunction with locomotor systems, sensory modalities guide coordinated feeding behavior, with vision playing an important role in many fishes. Although often studied separately, the locomotor, feeding and visual systems have not previously been examined together during fish feeding. To explore feeding coordination, we examined the kinematics of feeding behavior in two species of herbivorous parrotfish, *Sparisoma radians* and *Scarus quoyi*, which exhibit different single bite and repetitive bite strategies. Kinematic data on pectoral fin movements and body position show distinctive differences in strategies for the approach and post-strike motion between these species. *Sparisoma* and *Scarus* exhibited significant differences in the magnitude of jaw protrusion, time to maximum jaw protrusion, cranial elevation, and order of events in the feeding sequence. Oculomotor data show that both species

orient the pupil forward and downward directed at the site of jaw contact until 100 ms before the bite, at which point the visual field is rotated laterally. Combinations of kinematic variables show repeated patterns of synchrony (onset and duration) for the approach to the food (distance, velocity, eye movement), prey capture (eye movement, jaw movement, fin movement) and post-capture maneuvering (fin movement, distance). Kinematic analyses of multiple functional systems reveal coordination mechanisms for detecting and approaching prey and executing the rapid opening and closing of the jaws during acquisition of food. Comparison of the coordination of feeding, swimming and sensory systems among fish species can elucidate alternative coordination strategies involved in herbivory in coral reef fishes.

Key words: herbivory, kinematics, biomechanics, functional morphology, eye movements, sensorimotor integration, coral reef fish, parrotfish.

Introduction

Feeding and locomotion in fishes are complex, coordinated behaviors that employ multiple functional systems (skull, fins, body, tail) in order to perform the capture of prey or execute a locomotor maneuver. However, much of the research on animal function takes a single system approach, in which comparative morphological and kinematic studies focus on individual units such as the skull, the fins, or the axial locomotor system. Recent studies of skull mechanics have revealed the biomechanical basis of suction feeding (e.g. Ferry-Graham and Lauder, 2001; Ferry-Graham et al., 2001; Grubich, 2001; Svanbäck et al., 2002; Waltzek and Wainwright, 2003; Carroll, 2004), biting behaviors (Alfaro and Westneat, 1999; Ferry-Graham et al., 2001, 2002b) and differences between these feeding modes (Alfaro et al., 2001). Similarly, research on the morphology and kinematics of fin-based swimming has resolved many of the questions of pectoral fin propulsion in fishes (Westneat, 1996; Walker and Westneat, 1997, 2000, 2002a,b; Westneat and Walker, 1997; Walker, 1998; Drucker and Lauder, 2002, 2003;

Lauder and Drucker, 2002; Thorsen and Westneat, 2005). The interaction or coordination of multiple functional systems in the performance of important behaviors is a relatively unexplored area of research that may provide new insights into functional morphology.

Coordination is the process that integrates the movement of multiple morphological components of an organism to accomplish a specific task. As each musculoskeletal system is capable of a nearly infinite range of motions, the main objective of coordination is to create a functional relationship between components to reduce the possible range of motion to a narrower range of motion for the execution of a specific behavior (Bernstein, 1967; Turvey, 1990). In the context of feeding, coordination involves several functional units, such as locomotor systems that direct movement and posturing towards the prey item, sensory systems that detect and guide the animal to the prey, and feeding systems that capture and process the prey item.

Despite the clear relationship between feeding and swimming, only a few studies have specifically integrated functional systems in kinematic analyses in fishes. In the first detailed analysis of locomotor patterns and jaw movements in fishes, Rand and Lauder (1981) demonstrated that two patterns of jaw movement coordinated with two different types of body movement in pike. Webb (1984a) found that during feeding events in several species of freshwater predatory fishes, approach speed and maneuverability are dependent on morphology of the locomotor apparatus (paired fins vs body/caudal fin movement), while body angle of approach is not. Borla et al. (2002) demonstrated that fine-scale maneuverability in larval zebrafish is not dependent upon appendicular fins alone, but on a combination of body and caudal fin bending movements, termed fine axial control, to produce a unique swimming style during prey capture that differs from their normal swimming behavior. Other studies involving electromyography have looked at motor patterns underlying movement in combinations of functional systems, such as the firing of jaw and axial muscles during feeding and escape responses (Schriefer and Hale, 2004), or eye movements during continuous swimming (Harris, 1965).

The present study focuses on coordination between feeding systems and the mechanics of pectoral fin locomotion. Labrid fishes (including wrasses, parrotfishes and odacids; Westneat and Alfaro, 2005; Westneat et al., 2005) use their pectoral fins as their main propulsors (Webb, 1984b; Westneat, 1996) to produce a range of lift- or drag-based propulsion modes (Westneat, 1996; Westneat and Walker, 1997; Walker and Westneat, 2000, 2002b) that likely play an important role in feeding behavior. Accompanying the variety in swimming modes, parrotfishes exhibit browsing, scraping or excavating feeding strategies to consume algae or detritus (Ochavillo et al., 1992; Bruggemann et al., 1994; Streelman et al., 2002; Choat et al., 2004). The feeding modes of excavating and scraping correspond to specific patterns of cranial myology (e.g. Board, 1956; Bellwood and Choat, 1990; Bullock and Monod, 1997; Streelman et al., 2002) and motor patterns (Alfaro and Westneat, 1999). The diversity of swimming and feeding mechanisms among parrotfishes suggests that species with different feeding mechanics may employ different coordination strategies to optimize body movement and positioning for prey capture.

Sensory systems also play a role in the coordination of feeding. During feeding, fish eye movements follow predictable patterns, and tracking such movements can serve as a proxy for visual input during a behavior (Easter and Nicola, 1996, 1997; Rodriguez et al., 2001). While swimming, eyes of fishes exhibit compensatory movements to stabilize the visual field while the body moves (Trevvarthen, 1968; Collin and Shand, 2003), and there is a close relationship between the periodicity of ocular and locomotor muscle activity (Harris, 1965; Trevvarthen, 1968). In many fishes, vision serves as the primary source of sensory input used to guide prey capture and eye movement is quite dramatic before and during the feeding strike, indicating that visual input is important for prey acquisition (Pettigrew et al., 2000; Anisdon et al., 2001).

Labrid fishes are assumed to also rely heavily on vision while feeding, though studies of vision in wrasses have focused primarily on either morphology or visual pigment sensitivity (Munz, 1958; Baylor, 1967; Barry and Hawryshyn, 1999; Siebeck and Marshall, 2000; Lara, 2001), and not on oculomotor behavior (Tauber and Weitzman, 1969).

The goal of the present study is to provide a quantitative kinematic analysis of three systems: skull kinesis, locomotion and vision, during feeding behavior in parrotfishes. We ask two primary questions: (1) Are there repeated, stereotypic patterns of coordination between feeding, locomotor and oculomotor systems during a feeding event? Quantitative kinematic data on all three systems allow us to examine levels of variability vs stereotypy in multiple functional systems. (2) How do these coordination patterns differ between species with different feeding ecologies? To address these questions, we present data on feeding coordination in two species of parrotfishes with different scraping and browsing trophic strategies.

Materials and methods

Two species of parrotfishes, *Scarus quoyi* Valenciennes ($N=4$, standard length 10.31 ± 0.30 cm mean \pm S.E.M.) and *Sparisoma radians* (Valenciennes) ($N=3$, standard length 14.44 ± 1.50 cm) were trained to feed on benthic food sources in aquaria. *Scarus quoyi* were purchased from a local tropical fish wholesaler, and *Sparisoma* were collected in otter trawls from Dog Island Reef, FL, USA, and shipped back to Chicago. Members of the Atlantic genus *Sparisoma* consume sea grasses (Lobel and Ogden, 1981; Bernardi et al., 2000), while members of the pantropical genus *Scarus* scrape algae, detritus and bacterial mat from coral heads (Bellwood and Choat, 1990; Ochavillo et al., 1992). During a feeding bout, *Scarus* makes more bites with a higher bite rate than *Sparisoma* (Bruggemann et al., 1994).

The manner in which prey is presented in analyses of feeding can strongly influence the behavior and resulting kinematics (Ferry-Graham et al., 2001). *Scarus* were fed commercially prepared frozen algae (Emerald Entrée, Sally's Bay Brand, Newark, CA, USA) spread on a round piece of a faviid coral skeleton, and *Sparisoma* were fed small pieces of lettuce anchored to the bottom of the tank, extending to the same height as the coral head treatment. We experimented with standardized prey types, but neither species would consistently and naturally feed on the preferred food presentation of the other species. *Sparisoma* would not eat the algal smear, and *Scarus* would only occasionally and passively nip at the small piece of lettuce. The feeding preference of these species thus required that we offer them slightly different versions of immobile vegetable matter, while accounting for as many aspects of the prey presentation as possible, including height, distance and angle of prey. Trained feeding behaviors of both species did not seem to differ from natural feeding behaviors observed in the wild (when observed on SCUBA).

Feeding behaviors were filmed using a digital high-speed video camera (MotionScope, Redlake Imaging, San Diego,

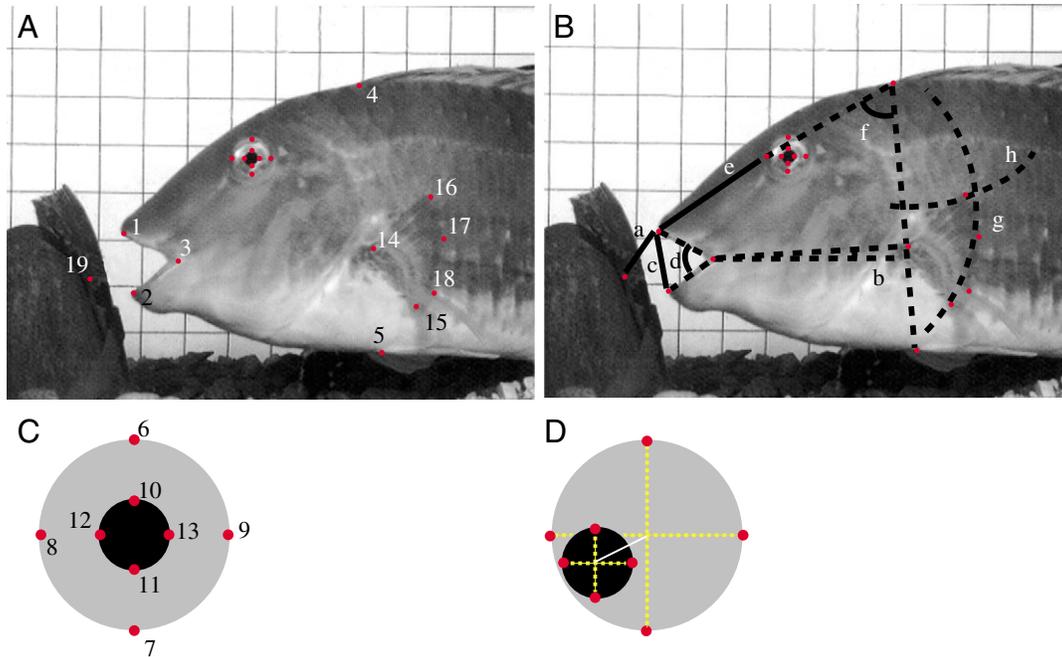


Fig. 1. (A,C) Morphological landmarks used. (1) Tip of premaxilla, (2) tip of dentary, (3) quadrate–articular joint, (4) anterior base of dorsal fin, (5) anterior base of pelvic fin, (6–9) orbit, (10–13) pupil, (14) leading edge base of pectoral fin, (15) trailing edge base of pectoral fin, (16) leading tip of pectoral fin, (17) middle edge of pectoral fin, (18) trailing tip of pectoral fin, (19) food item. (B,D) Kinematic variables calculated from morphological landmarks: distance to prey (a), body angle of approach (b), gape (c) and gape angle (d), jaw protrusion (e), cranial elevation (f), fin abduction (g), fin protraction (h). Solid lines indicate distances, broken lines indicate angles. (C) Morphological landmarks plotted to estimate the center of the orbit and pupil; (D) pupil vector (distance and angle) measured using the estimated centers.

CA, USA) at $250 \text{ frames s}^{-1}$. Only sequences with a lateral view where the fish could be clearly seen were analyzed (4 events recorded for each *Scarus*, 2–3 events for each *Sparisoma*). A scale-bar was placed over the food item before the feeding trial to accurately calibrate length in the digitized footage. Digital video footage was exported as an image sequence (Apple Quicktime), and imported into TPSdig (Rohlf, 2003). On each frame of the video sequence, 19 morphological landmarks were plotted on each image in order to quantify the movements of the jaws, fins, eyes and body of fishes during feeding (Fig. 1A). Landmarks were (1) tip of premaxilla, (2) tip of dentary, (3) quadrate–articular joint, (4) anterior base of dorsal fin, (5) anterior base of pelvic fin, (6–9) limits of the orbit, (10–13) limits of the pupil, (14) leading edge base of pectoral fin, (15) trailing edge base of pectoral fin, (16) leading edge tip of pectoral fin, (17) trailing edge of median fin ray of the pectoral fin, (18) trailing tip of pectoral fin, (19) food item (point closest to the animal).

Based on the movement of these landmarks, kinematic variables were calculated (Fig. 1B) using a series of algorithms in a custom-written kinematics program (CodeWarrior Pascal, Metrowerks Corporation, Austin, TX, USA) on an Apple Macintosh G5. Variables included distance to prey (linear distance between points 1, 19), body angle of approach (angle created by the line 3, 14, relative to horizontal), gape (distance between points 1 and 2), gape angle (angle 1, 3, 2), jaw protrusion (distance between points 1, 8), cranial elevation

(angle 8, 4, 5), pupil distance from the center of the eye (distance between the calculated centers of points 6–9 and 10–13), and pupil angle (angle between the calculated centers of points 6–9 and 10–13, relative to the fish's horizontal axis).

Velocity and acceleration were calculated as first and second derivatives of time and distance using the QuickSAND program (Walker, 1997, 1998), and smoothed using the predicted mean square error quintic spline (Walker, 1998). The time that the fishes first reached the food item was defined as the time of the shortest distance to the food item, designated as t_0 and indicated as a broken line on kinematic plots. Protraction and abduction of pectoral fin movement were calculated from the maximum length of the leading edge of the pectoral fin. Once the maximum length of the fin was determined, we calculated the projected length (based on the apparent length of the fin ray) into the z -plane as well as the angle relative to the body using the law of cosines. Stroke plane angle of the pectoral fins was calculated using the x,y coordinates of the pectoral fin tip at the beginning and end of a downstroke. The angle of this line (relative to horizontal) was then subtracted from the body angle to make the stroke plane angle relative to the fishes' body position. For comparison, all sequences were aligned based on t_0 . Variables are plotted as mean \pm S.E.M.

Coordination of feeding, locomotion and vision was assessed in three ways. First, we tested for differences between species in single timing variables. Magnitude, time to maxima,

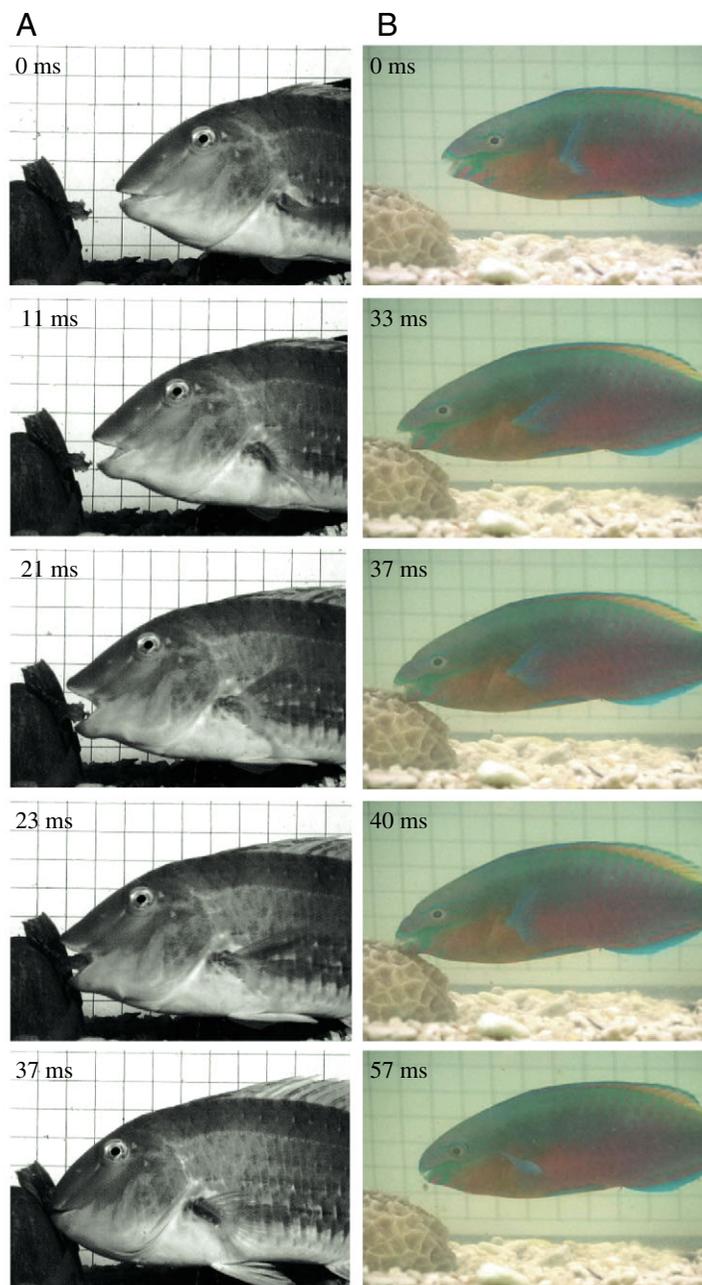


Fig. 2. Representative feeding sequences of (A) *Sparisoma radians* and (B) *Scarus quoyi*. Timings of events (in ms) are indicated.

and event duration of the kinematic parameters were analyzed using a nested ANOVA to test for potential differences between individuals and species, using the JMP version 5.0.1.2 statistical package (SAS Institute, Cary, NC, USA). Gape and velocity parameters were scaled by standard length in statistical analyses to account for the slightly larger size of the *Sparisoma* individuals. Second, the overall pattern of coordination was assessed by comparing the kinematic variables from the three functional systems relative to the time during the feeding strike. Third, we examined the stereotypy of kinematic variables to assess the degree to which feeding

coordination was repeated in a similar way from one feeding (or individual) to the next. Stereotypy of feeding strikes was assessed by calculating the coefficient of variation (CV) for each individual animal (Schleidt, 1974; Barlow, 1977), and then pooled for each species to better account for individual variability (Barlow, 1977). We predicted that most cranial kinematics and eye motion would be stereotypic, with CV less than 1.0, whereas features of fin motion and locomotor and cranial timing would have higher variability.

Results

Kinematics of feeding coordination

Both species of parrotfishes exhibited repeated and largely stereotypic patterns of movement and coordination during feeding strikes (Fig. 2). The two species exhibited significant differences in the magnitude of jaw protrusion, time to maximum jaw protrusion, cranial elevation, magnitude of pectoral fin protraction during breaking, as well as the overall order of events during the feeding sequence (Table 1). There were no significant differences among individuals within species for feeding parameters, so individual effects were not explored further. Approach velocities ranged from 6 to about 16 cm s^{-1} in the two parrotfishes (Fig. 3A,B), and length-specific approach velocities were not significantly different between species. However, *Scarus* exhibited an increase in velocity post prey capture, as the fish moved away from the food item (Fig. 3B), while *Sparisoma* usually came to a stop and did not move away from the food after prey capture. There were no significant differences in the magnitude of maximum acceleration (Fig. 3C), although the two species slow down at different times during the approach. Both species maintained negative body angles of approach (head pointing down) towards the food item (Fig. 3D), though *Sparisoma* increased and then decreased this body angle, while *Scarus* only decreased the approach angle when close to prey contact.

Gape distance and gape angle were similar between the two species (Fig. 4A,B). Both magnitude and timing of jaw protrusion were significantly higher in *Scarus* (Fig. 4C); *Scarus* also exhibited a second period of jaw protrusion associated with food handling following capture. Strike duration did not differ significantly between the two species (*Sparisoma*, $0.208 \pm 0.012 \text{ s}$; *Scarus*, $0.204 \pm 0.016 \text{ s}$). *Sparisoma* typically conducted one bite on the food item and then paused for processing, while *Scarus* exhibited up to five successive bites per feeding bout before pausing for processing. During the strike, cranial elevation was not always present, but when it occurred it was significantly greater in *Scarus* than *Sparisoma* (Fig. 4D).

Approach to the prey was a combination of gliding, using previous momentum from unrecorded fin strokes, as well as several pectoral fin beats within the field of view, with *Sparisoma* performing more fin beats over the approach time period than *Scarus*. For both pectoral fin abduction and

Table 1. Results of statistical comparisons between *Sparisoma radians* and *Scarus quoyi* for kinematic variables during feeding, tested with a two-way analysis of variance

Variable	<i>Sparisoma</i>		<i>Scarus</i>		F ratio	P
	Mean	CV	Mean	CV		
Body movements						
Maximum velocity ($BL\ s^{-1}$)	1.117±0.151	0.30±0.19	0.949±0.116	0.37±0.13	0.5166	NS
Time to maximum velocity (s)	-0.0533±0.0151	0.73±0.47	-0.184±0.0412	0.81±0.33	2.4304	NS
Time to max. acceleration (s)	-0.0213±0.0158	4.97±4.78	0.00133±0.00421	1.55±0.74	1.2149	NS
Maximum acceleration ($cm\ s^{-2}$)	346.19±41.69	0.10±0.05	413.743±78.341	0.36±0.14	0.3182	NS
Change in body angle (deg.)	14.94±2.55	0.36±0.06	10.50±1.77	0.39±0.21	8.5438	**
Gape						
Gape (cm)	1.2406±0.1098	0.19±0.14	0.8677±0.0433	0.14±0.05	4.6587	*
Adjusted gape ($cm\ BL^{-1}$)	0.0878±0.0252	0.19±0.14	0.0830±0.0038	0.14±0.05	1.4092	NS
Gape duration (s)	0.208±0.012	0.17±0.06	0.204±0.016	0.27±0.07	1.7107	NS
Time to max. gape (s)	-0.0807±0.1371	0.19±0.14	-0.0425±0.0093	0.14±0.05	2.5421	NS
Gape angle (deg.)	86.863±5.781	0.10±0.04	100.752±4.323	0.13±0.04	2.4948	NS
Jaw protrusion						
Jaw protrusion (cm)	0.0191±0.0063	1.47±0.08	0.0374±0.0039	0.61±0.20	5.5941	*
Jaw protrusion duration (s)	0.176±0.0393	0.27±0.24	0.1471±0.0112	0.41±0.13	4.5914	*
Time to max. jaw protrusion (s)	-0.1376±0.0286	0.11±0.12	-0.0480±0.01776	0.26±0.08	1.1171	NS
Cranial elevation						
Cranial elevation (deg.)	0.7332±0.1211	0.96±0.19	1.160±0.082	0.68±0.17	8.5101	**
Cranial elevation duration (s)	0.232±0.0237	0.14±0.08	0.1592±0.0250	0.23±0.07	1.0100	NS
Time to max. cranial elevation (s)	-0.0667±0.0471	0.13±0.08	-0.1748±0.0320	0.36±0.11	1.7856	NS
Eye movement						
Maximum eye movement (cm)	0.0913±0.0101	0.29±0.17	0.1137±0.0147	0.39±0.17	1.9595	NS
Eye movement duration (s)	0.1973±0.0257	0.31±0.16	0.1502±0.0173	0.32±0.11	1.2530	NS
Time to maximum eye movement (s)	-0.1733±0.0291	0.21±0.15	-0.1785±0.0394	0.44±0.11	1.1358	NS
Pectoral fin movement						
Cruising						
Protraction magnitude (deg.)	37.384±7.5413	0.45±0.03	48.0137±16.1412	0.40±0.09	0.7851	NS
Protraction duration (s)	0.1296±0.021	0.42±0.22	0.164±0.0609	0.62±0.25	0.2778	NS
Abduction magnitude (deg.)	55.187±7.6716	0.32±0.1268	49.1985±4.6961	0.26±0.06	0.0781	NS
Abduction duration (s)	0.1808±0.0484	0.43±0.3804	0.2453±0.0398	0.09±0.10	0.6748	NS
Braking						
Protraction magnitude (deg.)	48.2706±12.1341	0.31±0.07	85.1625±8.3506	0.37±0.13	10.595	*
Protraction onset (s)	-0.028±0.0205	1.57±0.96	-0.0386±0.0104	0.85±0.27	0.0539	NS
Protraction duration (s)	0.0933±0.0209	0.54±0.30	0.1126±0.0098	0.31±0.14	0.0462	NS
Abduction magnitude (deg.)	41.8746±9.5154	0.55±0.28	46.0302±4.923	0.18±0.09	0.3334	NS
Abduction onset (s)	-0.0608±0.025	0.66±0.62	0.0032±0.013	3.88±2.28	2.7195	NS
Abduction duration (s)	0.1104±0.0245	0.35±0.42	0.0664±0.0079	0.22±0.06	1.1101	NS

BL, body length.

Spatial and temporal kinematic values are means ± S.E.M., and the variability of these parameters is represented by the mean coefficient of variation ($CV \pm S.E.M.$) taken from individuals and pooled for each species.

NS, $P > 0.05$; * $P < 0.05$; ** $P < 0.01$. There were no significant intraspecies differences.

protraction, these species exhibited similar ranges of cruising fin movements (*Sparisoma*: abduction, $55.187 \pm 7.6716^\circ$; protraction, $37.384 \pm 7.5413^\circ$; *Scarus*: abduction, $49.1985 \pm 4.6961^\circ$; protraction, $48.0137 \pm 16.1412^\circ$). *Sparisoma* cruising fin beat cycles took 0.1808 ± 0.0484 s, *Scarus* cruising fin beat cycles took 0.2453 ± 0.0398 s (Table 1).

Both species brake strongly just before biting. A sweeping fin stroke, down and forward, served as a braking maneuver

that produced a large decrease in velocity. Braking kinematics of two representative feeding events (Fig. 5A) show that the pectoral braking stroke begins before t_0 (prey contact) and extends through the feeding event. Mean braking stroke plots (Fig. 5B) illustrate that *Scarus* pectoral fins exhibit a significantly larger magnitude of fin protraction during braking ($85.1625 \pm 8.35^\circ$, reaching up to 165°) than *Sparisoma* ($48.287 \pm 12.1341^\circ$) when the fish bites the food item. The

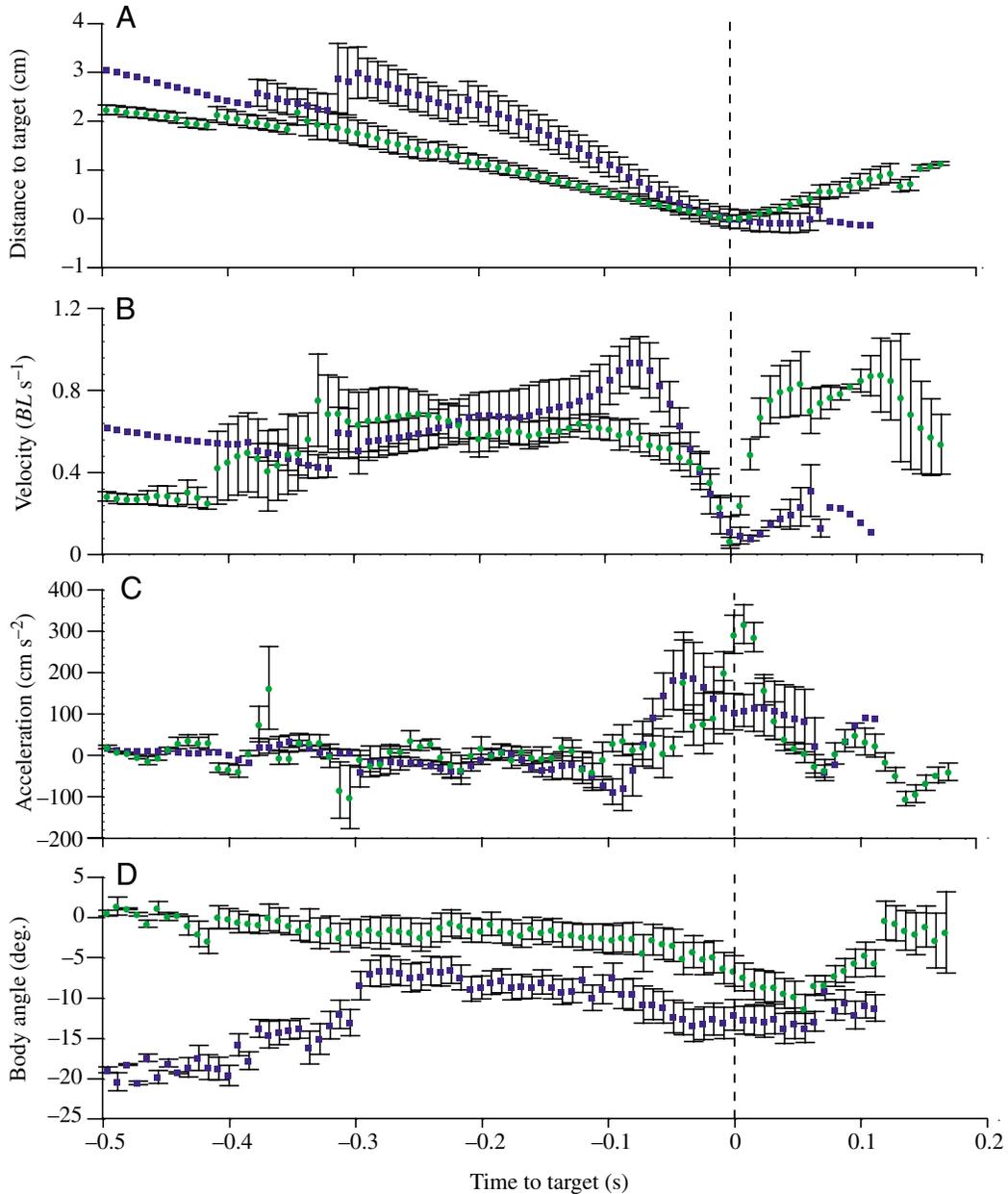


Fig. 3. Kinematic plots of body movement during the feeding strike in *Sparisoma radians* and *Scarus quoyi*. (A) Distance to prey target (cm), (B) velocity ($BL\ s^{-1}$), (C) acceleration ($cm\ s^{-2}$) and (D) body angle of approach (degrees) vs time for *Sparisoma radians* (blue squares) and *Scarus quoyi* (green circles). Contact with food item occurs at t_0 , indicated by broken vertical lines.

stroke plane angle differed between cruising and braking pectoral fin strokes (Fig. 5C), with *Sparisoma* sweeping the fins through stroke plane angles for cruising and braking of $70.3 \pm 7.7^\circ$ and $30.7 \pm 6.8^\circ$, respectively; *Scarus* cruising was also significantly higher during cruising ($67.9 \pm 5.5^\circ$) than braking ($34.4 \pm 4.4^\circ$).

Eye movements of the two species followed similar patterns. Upon approach to the prey, the eye was shifted towards the prey item (*Sparisoma*: 0.0913 ± 0.0101 cm at 173.3 ± 29.1 ms to prey capture; *Scarus*: 0.1137 ± 0.0147 cm at 178.5 ± 39.4 ms to prey capture), then at approximately 100 ms before food capture the pupil shifted back to a centered position (Fig. 6A).

There were no significant differences in either the magnitude or the timing of pupil movement between *Sparisoma* and *Scarus*. Pupil movement in both species was forward and slightly downward during the approach in the direction of the prey item. *Sparisoma* pupils were focused between 0 and -5° (looking slightly downward), while *Scarus* pupils were focused farther ventrally between -5 and -15° during the approach to the food item (Fig. 6B). At -0.05 s, *Scarus* pupils returned to a mostly centered position for the bite. When pupil distance is plotted against distance to the food item (Fig. 6C), *Sparisoma*'s eyes shifted to center (2 cm to food contact) before those of *Scarus* (1 cm to food contact).

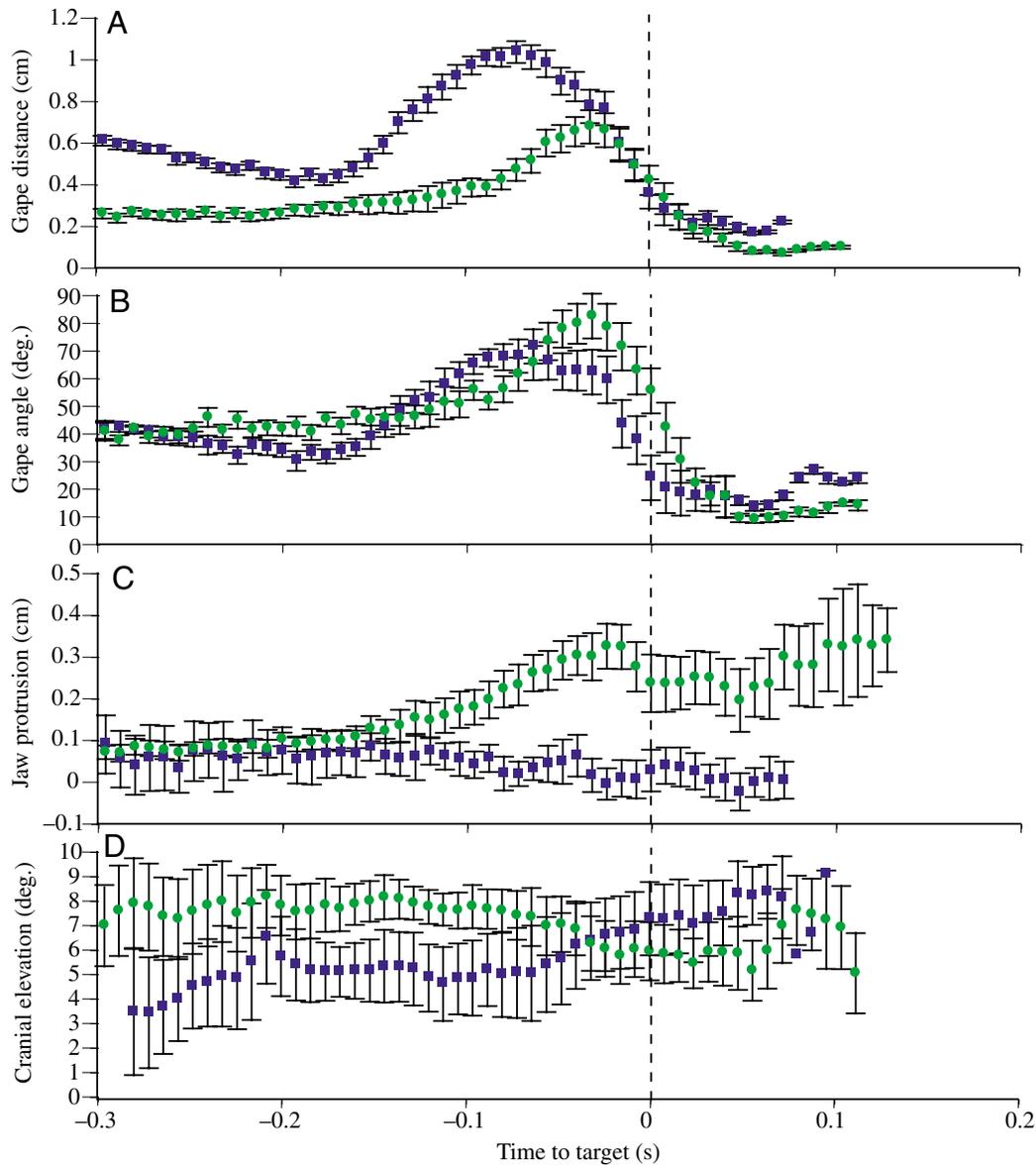


Fig. 4. Kinematic plots of jaw and head movements during the feeding strike in *Sparisoma radians* and *Scarus quoyi*. (A) Gape (cm), (B) gape angle (degrees), (C) jaw protrusion (cm), and (D) cranial elevation (degrees) vs time for *Sparisoma radians* (blue squares) and *Scarus quoyi* (green circles). Contact with food item occurs at t_0 , indicated by broken vertical lines.

Stereotypy and coordination profiles of feeding

The two species of parrotfishes exhibited similar levels of spatial and temporal variability of the kinematic components of the feeding strike (Fig. 7, Table 1). Most of the kinematic variables had a CV of less than one, but such features as time to maximum acceleration (Fig. 7A) and time to maximum cranial elevation (Fig. 7B) displayed a higher level of variation than other components of body movement, jaw, fin and eye movement (Fig. 7C,D). This overall low degree of variation in the features of the feeding strike suggests a similar degree of stereotypy for *Sparisoma* and *Scarus*, despite spatio-temporal differences in the patterns of coordination.

The timing of multiple events was consistently synchronized upon approach to the food item for both species. While there

are a large number of possible interactions between kinematic variables, we have chosen examples that illustrate the range of coordination exhibited in parrotfish feeding behavior. Both species used a broadside, braking pectoral fin downstroke just before prey contact that was correlated with a dramatic decrease in velocity (Figs 8A,D, 9A,D). During this deceleration event, the eyes of both species were shifting back to a center-orientation (Figs 8A,C and 9A,C). In *Sparisoma*, maximum attained velocity is synchronized with maximum gape (Fig. 8A,B), whereas *Scarus* does not exhibit the same degree of synchrony between these two parameters (Fig. 9A,B). For both *Scarus* and *Sparisoma* the maximum distance of the pupil from the center of the eye is synchronized with the onset of mouth opening, but the eyes are shifting to

center when the mouth fully opens (Figs 8B,C and 9B,C). In both species, maximum gape coincides with a large fin upstroke, and mouth closing is correlated with a fin downstroke (Figs 8 and 9).

Discussion

Scarus quoyi and *Sparisoma radians* exhibit stereotypic intraspecific patterns of body, jaw, fin and eye movements during the approach, strike and recovery phases of the feeding sequence. *Sparisoma* and *Scarus* exhibited significant differences in the magnitude of jaw protrusion, time to maximum jaw protrusion, cranial elevation, and order of events in the feeding sequence. We conclude that the pectoral fins of parrotfishes act as sources of thrust during the approach, as braking and maneuvering thrusters during the strike, and then again as forward propulsors after the strike. After prey contact the pectoral fins are swept forward in a braking maneuver, and post-strike pectoral fin motion is highly variable. We conclude that vision is the central sensory modality that mediates coordination of the approach to the feeding event. At approximately 100 ms before prey capture, the jaws open, and the eye position shifts back to center as the fish decelerates.

This indicates that the role of vision in feeding coordination ends before the strike, and vision may then play a role in other objectives such as predator detection. By examining these three motor systems in the context of feeding behavior, it is possible to quantify how they operate together in an organism, and how their coordination differs with diverse feeding strategies. Incorporating and analyzing multiple functional systems during the feeding behavior of fishes allows for quantification of the timing and magnitude of important functional events, as well as a better understanding of the interaction and synchronization of these components.

Coordination of skull, fins and eyes during fish feeding

Feeding in parrotfishes involves rapid biting of the substrate or algal prey with coordinated movement of the body, skull, jaws and pectoral fins, mediated primarily by the use of vision. The common features of feeding coordination in parrotfishes are evident in the timing patterns of kinematic parameters (Fig. 10), which can be divided into three primary phases. First, during the approach phase, when the fish is still greater than 300 ms from prey contact, both parrotfish species began to adjust cranial and locomotor features. Approach angle and pectoral fin motion were modulated to some degree but showed

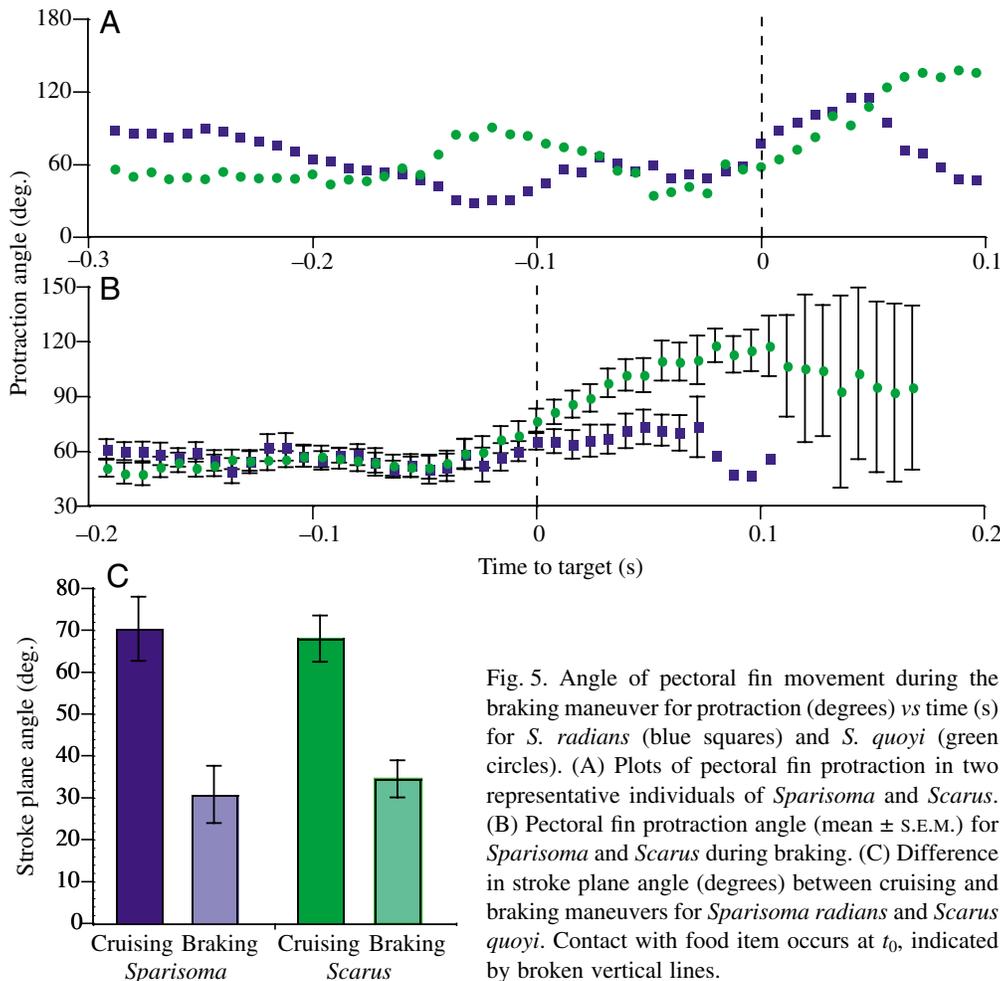


Fig. 5. Angle of pectoral fin movement during the braking maneuver for protraction (degrees) vs time (s) for *S. radians* (blue squares) and *S. quoyi* (green circles). (A) Plots of pectoral fin protraction in *Sparisoma* and *Scarus*. (B) Pectoral fin protraction angle (mean \pm S.E.M.) for *Sparisoma* and *Scarus* during braking. (C) Difference in stroke plane angle (degrees) between cruising and braking maneuvers for *Sparisoma radians* and *Scarus quoyi*. Contact with food item occurs at t_0 , indicated by broken vertical lines.

repeated patterns, with low CV (Fig. 7). The eyes of both species were maximally shifted forward at approximately 175 ms before prey contact, coinciding with a slight decrease in body angle. During the strike phase, from about 300 ms pre-contact until the bite, *Scarus* began to increase cranial elevation (peaking at 175 ± 32 ms), and at approximately 100 ms to prey contact, jaw protrusion increased (peaking at 37.3 ± 3.9 ms). *Scarus* onset of jaw opening occurred after the onset of jaw protrusion (though maximum gape occurred before maximum jaw protrusion at 42 ± 0.01 ms before prey contact). In contrast, *Sparisoma* delays cranial elevation until much later in the feeding cycle but initiates jaw opening earlier (Fig. 10). Most notable is the difference in the timing between the onset of jaw opening and the achievement of maximum gape between the two species. Jaw opening initiates the *Sparisoma* feeding sequence, followed by cranial elevation, and lastly jaw protrusion, whereas the *Scarus* sequence begins with cranial

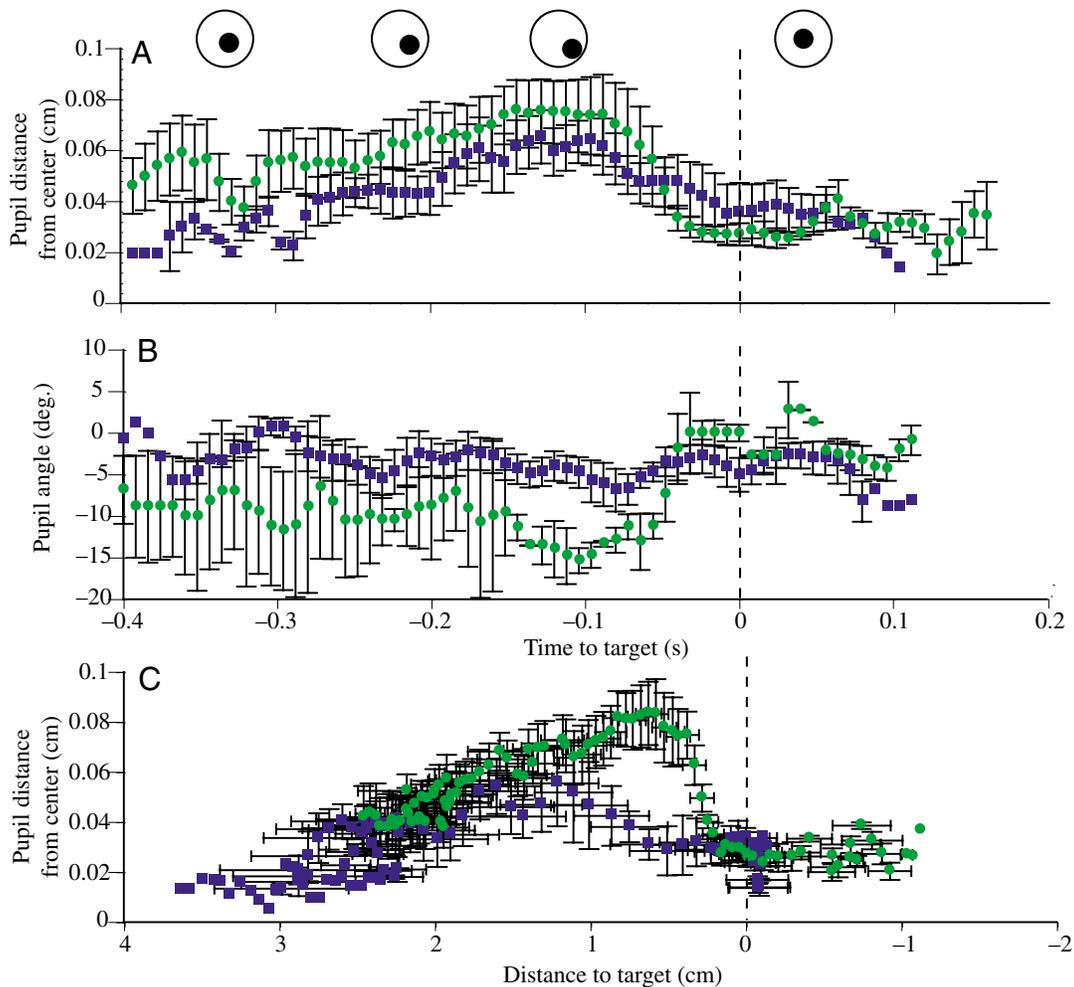


Fig. 6. Kinematic plots of eye movements during feeding strike in *Sparisoma radians* and *Scarus quoyi*. (A) Pupil distance from the center of the eye (cm) vs time, (B) pupil angle (degrees) vs time, and (C) pupil distance from the center of the eye (cm) vs distance from prey item (cm) for *Sparisoma radians* (blue squares) and *Scarus quoyi* (green circles). Pupil distances were smoothed with a three-point running average. Broken lines indicate contact with prey item.

elevation, followed by jaw protrusion and lastly maximal jaw opening (Fig. 10). Cranial kinematics were significantly different between species for the strike phase, with gape timing, magnitude of jaw protrusion, time to maximum jaw protrusion, cranial elevation and order of events in the feeding sequence showing interspecific differences.

These differences in coordination of the herbivorous bite may be due to differences in food type. *Sparisoma radians* eats mainly seagrass blades and epiphytes (Lobel and Ogden, 1981), while *Scarus quoyi* consumes mainly benthic turf algae and associated detritus and bacterial mat (Ochavillo et al., 1992). Due to the physical differences in the morphology of these food items, the associated functional demands of prey capture (browsing vs scraping) are consequently different for these two species and are reflected in their feeding behaviors. The blades of seagrass may be somewhat motile in areas with current, and by initiating mouth opening first, *Sparisoma* has attained maximum gape with the mouth having created a larger area for grabbing the seagrass blade to compensate for

potential minor movements of the grass. *Scarus* does not have this need as the benthic turf algae remains at a fixed point, and instead needs to exert more force during its bite to successfully scrape algae off of the coral head (Fig. 9D). Variability in cranial elevation in parrotfishes studied here was also noted in the EMG study of Alfaro and Westneat (1999) in which variable presence/absence of epaxial muscle activity was shown to be associated with variable cranial elevation in parrotfishes.

The two species also exhibited different patterns of pectoral fin movement during the feeding strike. During braking, *Scarus quoyi* pectoral fins primarily moved forward during braking (in protraction), whereas *Sparisoma radians* pectoral fins primarily moved downward (in abduction) for braking (Fig. 5, Table 1). The stroke plane angle in labriform swimmers may range from almost vertical to nearly horizontal, and this variable is a primary determinant of the mode of thrust production by the pectoral fin stroke (Walker and Westneat, 2000, 2002a). Though the data on stroke plane angle did not

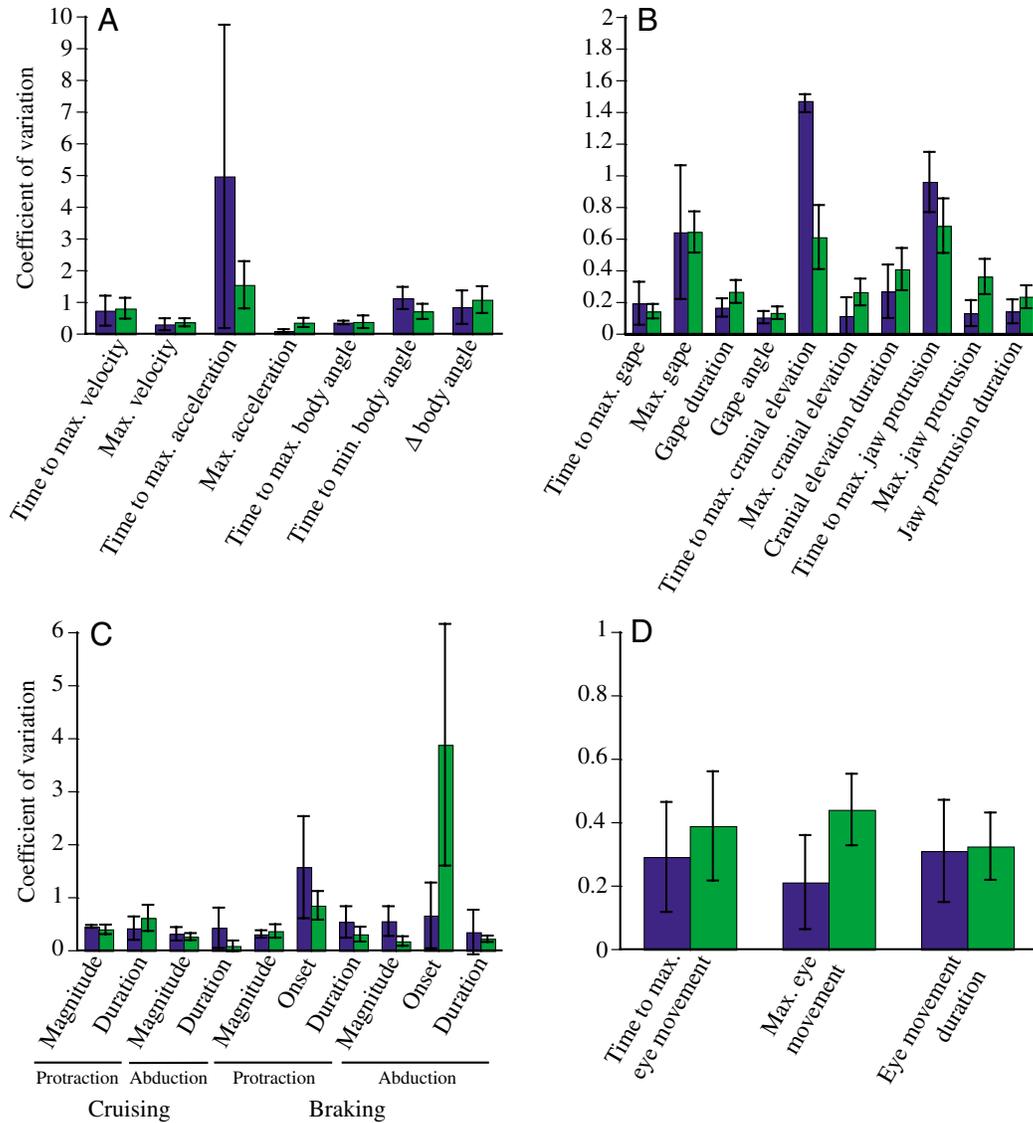


Fig. 7. Degree of stereotypy of the different components of the feeding strike for *Sparisoma radians* (blue) and *Scarus quoyi* (green) as a function of the coefficient of variation (CV) for (A) body movement and position, (B) jaw movement, (C) fin movement, and (D) eye movement, represented by mean CV \pm S.E.M. for each species. A larger CV represents higher variability.

appear to differ between species, further analyses of steady and unsteady state swimming of these species is needed to confirm differences in locomotor mechanics. *Scarus* has a significantly higher pectoral fin aspect ratio than *Sparisoma* (data from Wainwright et al., 2002; one-way ANOVA: d.f.=1, $F=14.8056$, $P=0.0009$). Fin morphology is a correlate of the type of labriform locomotion (drag or lift-based; Westneat, 1996; Westneat and Walker, 1997; Walker and Westneat, 2000, 2002a; Wainwright et al., 2002). These underlying differences in fin morphology and additional possible differences in musculature may contribute to differences in thrust production.

The pectoral fins provide thrust for two alternative goals of locomotion during feeding: maneuvering during feeding bouts and locomotion during foraging. The pectoral fin protraction

of *Scarus quoyi* during its bite has longer duration and greater magnitude than that of *Sparisoma* (Fig. 5B,C). The extended downstroke of *Scarus* may contribute a reactive force that helps move the jaws across the coral head during the scraping bite, increasing the efficiency of the scrape, as well as regulating the force of the collision between the jaws and the substrate. During many *Scarus* bites, it appears as though the fish is slamming its head into the rock, and force-plate technology would be an interesting tool to test this idea. For *Sparisoma* feeding on seagrass blades, the large braking maneuver is not as critical, as these plants do not present a hazard of collision, and *Sparisoma* will often swim into and through the sea grass blade as it bites (as seen in both field and laboratory feeding events). Additionally, *Sparisoma* may combine the motions of pectoral fin downstroke and head

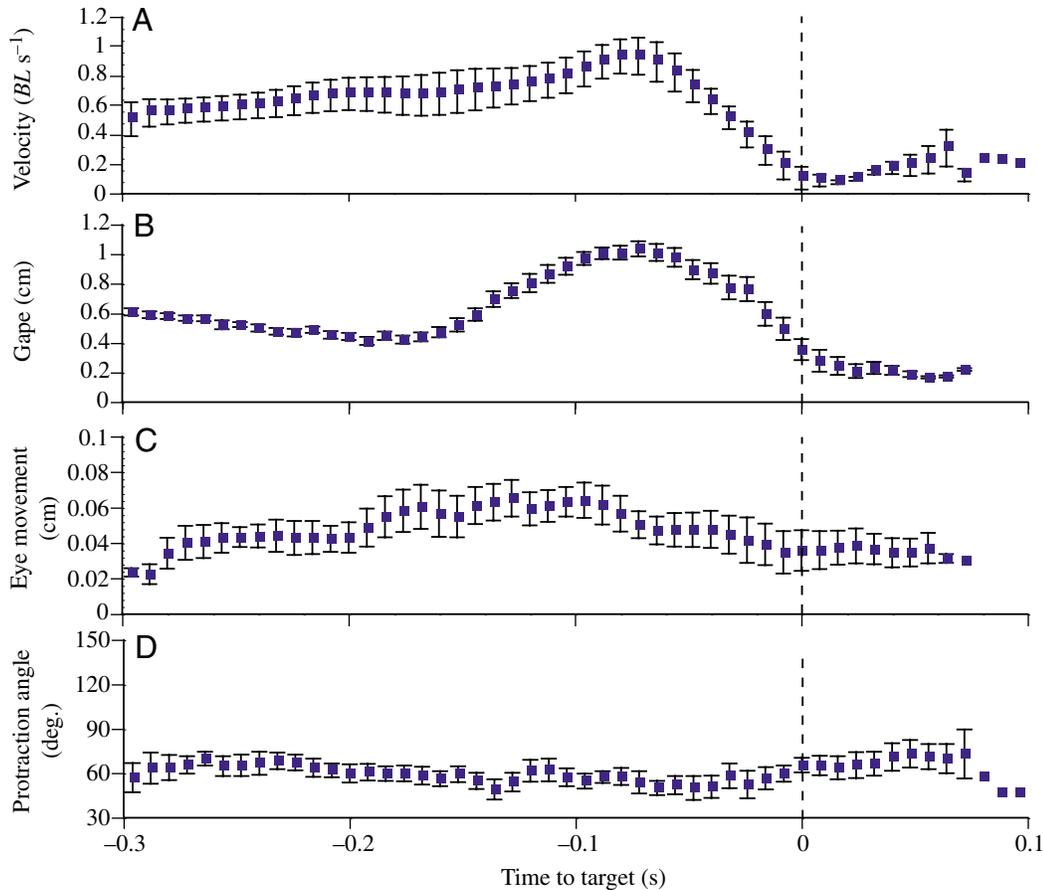


Fig. 8. Selected *Sparisoma radians* coordination variables, showing the kinematic relationships between different functional systems: (A) velocity ($BL\ s^{-1}$), (B) gape (cm), (C) eye movement (cm), (D) fin protraction (degrees) vs time to prey contact (s). Broken line indicates contact with prey item.

movement to help tear pieces from the blades of food. More broadly, the locomotor strategies may reflect the energetics required for foraging distances (Wainwright et al., 2002). The turf algae fed upon by *Scarus quoyi* is distributed irregularly across the reef flat and reef slope (e.g. Ochavillo et al., 1992), and consequently, the species would have to spend more time and cover more distance swimming while foraging. *Sparisoma* foraging in high density and broadly distributed beds of seagrass blades (Lobel and Ogden, 1981) may not need increased locomotor efficiency to cover large distances while feeding.

Although any musculoskeletal system of the body may be involved in coordinated behavior, such behaviors in vertebrates typically include the appendages, vertebrae and axial musculature, cranial morphology, and sensory organs involved in parallel control of movement and posture (Massion and Dufossé, 1988; Massion, 1992; Massion et al., 2003). Control of movements in any organism can either be microscopic or macroscopic in scale (muscle cells contracting vs appendicular or axial movements); simple or complex in scope (such as action within a single appendage to actions comprised of multiple appendages or body parts; Bernstein, 1967; Clarac, 1984; Turvey, 1990; Weiss and Jeannerod, 1998). Movements are guided by exteroceptive and/or proprioceptive sensory feedback and must be appropriately synchronized in both temporal and spatial domains for the task to succeed (Weiss

and Jeannerod, 1998; Cordo and Gurfinkel, 2003). For behaviors involving complex coordination, voluntary movements are often supported by involuntary ('associated') movements (Cordo and Gurfinkel, 2003); for example, movements that serve to adjust the center of gravity of the organism to compensate for changes in posture (Massion et al., 2003). The coordination of motor systems itself is not the end goal, but a means of successfully executing a behavior (Weiss and Jeannerod, 1998).

These principles of coordinated behavior can be used by the biomechanics community to collect data on multiple systems in important behaviors such as feeding and locomotion. For the herbivores studied here, coordinated execution of fin movement, body posture and jaw movement may be necessary for bouts of continuous feeding along the floor of the coral reef or sea-grass beds. Herbivorous reef fishes are suggested to have well-developed pectoral musculature to precisely move and orient the body during feeding events (Choat, 1991). Fishes in other trophic groups (i.e. piscivores and planktivores) also need to integrate these functional systems during feeding. However, we predict that the coordination of pectoral fins and their role in maneuverability are less important during the actual strike of a piscivore, but are prominent during stalking and again during braking after the strike. The combination of ram and suction feeding might be sufficient for successful prey capture and decrease the needed precision of body orientation,

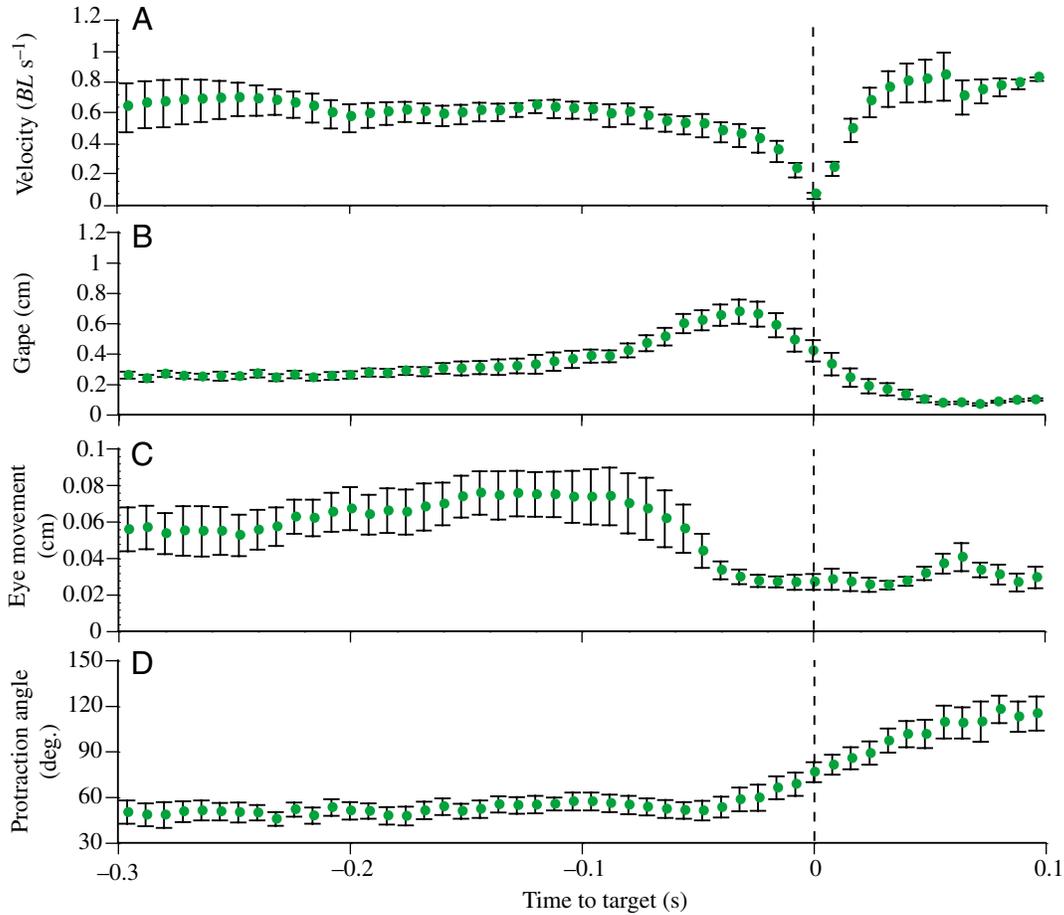


Fig. 9. Selected *Scarus quoyi* coordination variables, showing the kinematic relationships between different functional systems: (A) velocity ($BL s^{-1}$), (B) gape (cm), (C) eye movement (cm), (D) fin protraction (degrees) vs time to prey contact (s). Contact with food item occurs at t_0 , indicated by broken vertical line.

as prey items will be swept into the mouth by the accelerating flow field (Wainwright et al., 2001). Herbivores may require a finer level of precision in coordination in order to graze

effectively along substrata with varying topographies and at varying angles (Webb, 1984b). Bellwood (2003) suggested that the process of successful food procurement is the main constraint in the evolution of marine herbivores. Timing the braking maneuver of pectoral fin downstroke to coordinate with jaw closing will prevent fishes from colliding with their prey item, and the braking motion would also serve to lift the fish up and away from the food, allowing the fish to begin food processing, establishing a

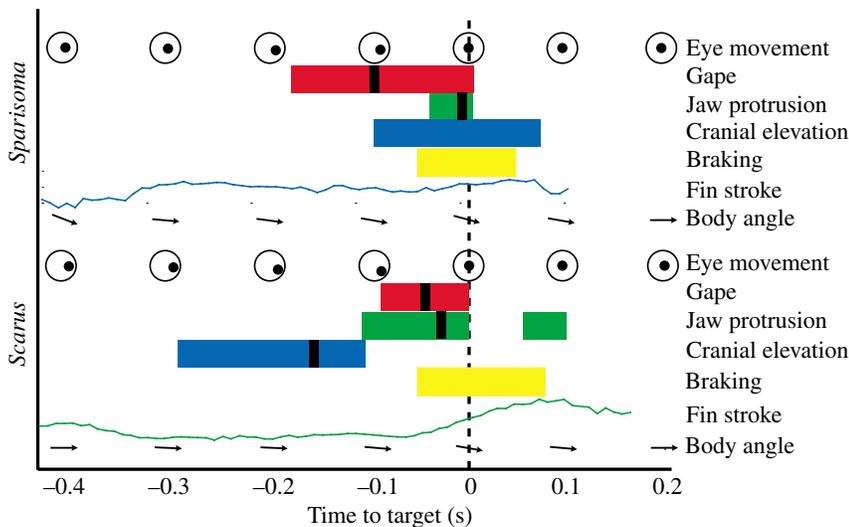


Fig. 10. Schematic representation of kinematic variables representing jaw, fin and eye movements during feeding behavior in *Sparisoma radians* and *Scarus quoyi*. Time period of activity for the variables is indicated by a horizontal colored bar. The maximum for each parameter is indicated by a solid black bar. Contact with food item occurs at t_0 , indicated by broken vertical line.

posture that promotes predator observation, and reorient to the next location for biting.

Coordination variability: is the herbivore's bite stereotypic?

Because food type was not altered during these experiments, no dramatic variations in feeding behaviors were observed (Fig. 7), but the subtle differences in feeding mechanics again demonstrate that herbivores have a range of biting styles (Bellwood and Choat, 1990; Alfaro and Westneat, 1999; Alfaro et al., 2001). The kinematic parameters of velocity (Figs 3A, 7A), body angle (Figs 3D, 7A), gape distance (Figs 4A, 7B), gape angle (Figs 4B, 7B) and jaw protrusion (Figs 4C, 7B), fin downstroke (Figs 5B, 7C) and eye movement (Figs 6, 7D) show a relatively low amount of variability, and thus a high degree of stereotypy, while acceleration (Figs 3C, 7A), cranial elevation (Figs 4D, 7B), and the fin beat cycle (Figs 5, 7C) reveal high degrees of variability. Jaw and eye movements appear to be stereotypic during the feeding sequence for each species, along with certain features of fin movements (i.e. braking downstroke), as evidenced by the low variance at individual time points. Alfaro and Westneat (1999) demonstrated variation in the motor pattern of jaw muscles during feeding between *Scarus iseri* and *Cetoscarus bicolor*, particularly during the multiple bite bouts of *S. iseri*. In the present study we found low variability in the feeding movements in *Scarus quoyi* and *Sparisoma radians*; electromyography data are now being sought to further test the stereotypy of the motor pattern.

The variability of fin movements might serve as a part of feedback modulation (*sensu* Deban et al., 2001): final adjustments to ensure proper body position and speed at the point of contact, before a feed-forward motor program is triggered for the biting behavior. Such modifications of movement would explain the lack of stereotypic patterns of fin beat patterns during the approach to the prey item. Only the approach and initial bite were examined for the two species; the bites for each species appeared to be stereotypic, as opposed to the two different bites utilized by *Scarus iseri* (Alfaro and Westneat, 1999). Future studies will analyze the kinematics and coordination of multiple bites in *Scarus quoyi* to test for stereotypy or functional versatility in the repeating bite mode. Exploring the effect of differences in food type (Sanderson, 1991) or ontogenetic stage (Reilly, 1995; Cook, 1996; Deban and Dicke, 1999) will further reveal the degree of relative stereotypy of the feeding behavior of these species.

Intergeneric differences between the feeding behaviors of these parrotfishes further demonstrates the evolutionary plasticity in the labrid feeding mechanism (Alfaro and Westneat, 1999; Alfaro et al., 2001), and provides supporting evidence for the hypothesis that differences in feeding ecology are responsible for early diversification among the parrotfishes (Streelman et al., 2002). This difference is probably amplified by specialization on different food types (Liem, 1978, 1979). Such modulation of feeding behaviors may have allowed for the expansion into and specializations for different trophic niches (Streelman et al., 2002), and observed differences in

feeding behaviors, such as differences in bite rate between *Scarus* and *Sparisoma* (Lobel and Ogden, 1981; Bellwood and Choat, 1990; Ochavillo et al., 1992), may reflect behavioral or physiological adaptations to nutritional differences in food quality (e.g. Choat, 1991; Choat and Clements, 1998; Choat et al., 2002).

The role of vision in parrotfish feeding

For both species of parrotfishes, a shift in pupil position from forward-looking (at the prey) to centered (viewing the environment) occurred well before actual contact with the food item: approximately 100 ms and 1.75 cm for *Sparisoma*, and 100 ms and 1 cm from the food item for *Scarus* (Fig. 6). The parrotfish *Cryptomus roseus* has a temporal foveal depression (Ali and Anctil, 1976), suggesting that the near field of vision in parrotfishes is in increased focus during the approach to the food item (Fernald and Wright, 1985; Fernald, 1990). In fishes with specialized areas of the retina, eye movements indicate the visual field of the fish and where the fish is looking (Collin and Shand, 2003). This analysis of eye movement suggests that although vision is used for guidance to the prey item, it is not involved in the final execution of the bite. As the parrotfish gets close to the food item, the jaws or snout of the fish may block the visual field of the laterally positioned eyes (e.g. Tamura, 1957), necessitating the use of other senses for final prey capture. Sensory input in this close range may be primarily mediated by the lateral line (Liem, 1978; Janssen and Corcoran, 1993; New et al., 2001; Montgomery et al., 2002). Future work exploring the details of the structure and function of the parrotfish eye will elaborate the role of the visual system in the coordinated behavior of these fishes.

The observed lateral eye movement back to a centered position (Fig. 6) may additionally serve as a mechanism for predator detection. Parrotfish are vulnerable to predation (e.g. Randall, 1967; Overholtzer and Motta, 2000), and their head-down foraging position further increases this vulnerability (Krause and Godin, 1996; Overholtzer and Motta, 2000). Scarids may also have to avoid attacks from territorial damselfishes when they feed on algae within their territories (Ogden and Buckman, 1973). Thus, when vision is no longer needed for guidance to a prey item, rapid eye movements may serve as the first line of defence against predators or attackers (Endler, 1986).

Ecomorphology and evolution of multiple functional systems

As the goal of ecomorphology is to link morphology to ecology through organismal performance (e.g. Wainwright, 1994, 1996), combined analysis of the behavior of multiple functional morphological systems may provide a more accurate estimation of the animal's abilities. Many previous studies of ecomorphology have focused on a single functional system such as the jaws or fins (e.g. Liem, 1978; Westneat, 1995; Wainwright, 1996; Wainwright and Bellwood, 2002; Wainwright et al., 2002), though it is becoming increasingly clear from this study and others that it is the combination and interaction of these functional systems that truly determines an

animal's ecology (Ferry-Graham et al., 2002a; Wainwright et al., 2002). Ferry-Graham et al. (2002a) stated that when foraging, an organism has to deal with a series of ecological 'filters', which ultimately determine if and how the organism forages. The animal has to detect a potential food item (sensory systems), it has to be able to arrive at the food item (locomotion), and then consume the item (feeding). In the context of coordination, we suggest that as the organism feeds, these filters continually place constraints on behavior, and the interaction of these filters results in coordination. Simultaneous analysis and quantification of multiple components of coordinated behavior may elucidate the interface between functional morphology, biomechanics and feeding ecology.

Despite the once-perceived functional homogeneity of herbivorous fishes (see Choat, 1991), comparative studies are demonstrating diversity and specializations for niche partitioning in these fish groups (Bruggemann et al., 1994). Coordination analysis may provide a complementary and integrative approach to previous studies of parrotfish feeding morphology (Board, 1956; Tedman, 1980a,b; Clements and Bellwood, 1988; Bellwood and Choat, 1990; Monod et al., 1994; Bullock and Monod, 1997), locomotor morphology (e.g. Westneat, 1996; Bellwood and Wainwright, 2001; Wainwright et al., 2002), ecology (Ogden and Buckman, 1973; Lobel and Ogden, 1981; Ochavillo et al., 1992; Bruggemann et al., 1994) and evolution (Bellwood, 1994; Bernardi et al., 2000; Streebman et al., 2002). By placing swimming, feeding and sensory function in the same context of feeding behavior, it is possible to document alternative combinations of functional parameters that might provide further axes of diversification between organisms that share a similar food source.

Similarly, coordination analysis holds promise for exploring the feeding strategy of closely related species in different trophic guilds. Within the Labridae, the parrotfishes represent one end of the trophic ecology continuum (Westneat, 1995; Wainwright and Bellwood, 2002; Wainwright et al., 2004). Thus, a comparison of how these functional systems interact in species of this family that consume different prey types may elucidate coordination differences necessary for different trophic niches. Additionally, further comparisons of sensory system function between fishes of different trophic types may reveal the functional constraints of particular feeding strategies, such as prey detection vs predator detection. Analyses of multiple functional systems within the context of coordination during feeding behaviors will further reveal axes of differentiation for feeding ecology in sympatric species to partition trophic resources within a community.

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