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Functional ecology of feeding in elasmobranchs

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Abstract Feeding behavior in the species of captive chondrichthyans is studied to clarify the functional mechanisms responsible for feeding ecology. Kinematics and pressure in the buccal, hyoid and pharyngeal regions were quantified in *Squalus acanthias*, *Chiloscyllium plagiosum* and *Leucoraja erinacea* using sonomicrometry and pressure transducers. Means and coefficients of variation were analyzed by species and by behavior to test for stereotypy and flexibility in the feeding mechanism. Several instances of mechanical stereotypy as well as flexibility were found in the feeding kinematics and pressure of the three chondrichthyan species. In general, *Squalus acanthias* shows more stereotyped feeding behavior than *C. plagiosum* and *L. erinacea*. Different aspects of feeding behavior stand out among the three species. *Chiloscyllium plagiosum* generates lowest pressures, *S. acanthias* achieves the greatest area changes, and *L. erinacea* has longer durations for manipulating prey. Capture events are functionally and behaviorally stereotyped while processing events are functionally and behaviorally flexible with the ability to use suction or compression to process the same food item. *Squalus acanthias* is a functional specialist and *C. plagiosum* is functionally a generalist, with both species exhibiting behavioral flexibility. *Leucoraja erinacea* is a functional and behavioral generalist. Using functional morphology to explain mechanical stereotypy and flexibility in the feeding behavior of three suction feeding chondrichthyan species has allowed a better understanding of specialist and generalist trophic behaviors.

Keywords Functional morphology · *Chiloscyllium* · *Leucoraja* · *Squalus* · Sonomicrometry · Pressure

Introduction

Studies on the feeding ecology of chondrichthyans necessarily focus on diet and trophic relationships due

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to the difficulty of capturing natural feeding events on film (Devadoss 1986; Cortés 1999; Ebert and Bizzarro 2007; Ebert et al. 2008; see also most papers in this issue). However, innovative techniques used to study feeding events in captive chondrichthyans can clarify the mechanisms responsible for feeding behaviors and thus have great potential to better understand the behavioral interactions underlying natural feeding ecology (Ferry-Graham et al. 2002; Dean et al. 2005; Gerry et al. 2008, 2010; Motta 2004; Wilga et al. 2007; see also Bizzarro et al. in review; Demski in review; Gardiner et al. in review; in this issue). As these techniques become more prevalent, studies are emerging that attempt to explain interspecific differences in the ecology and mechanics of feeding behavior in chondrichthyans (Ferry-Graham et al. 2002; Wilga et al. 2007; Gerry et al. 2008, 2010; Gerry and Scott 2010; Wilga 2010). These studies have primarily focused on generalist and specialist trophic ecology and feeding behavior in order to understand how and why different species capture various kinds of prey.

Stereotypical behaviors suggest that some kind of specialization is present and is a measure of how variable a behavior is in comparison to another species tested under the same condition (i.e. range of variation) (Ferry-Graham et al. 2002; Wainwright et al. 2008). The coefficient of variation represents a value for variation that is independent of the mean; dividing the standard deviation by the mean removes the correlation of the mean to the variance leaving a relative value for variation (Barlow 1977; Wainwright et al. 2008). For example, a species that has a narrow range of suction pressures around the mean might have a coefficient of variation (CV) of 0.5 and would be considered more stereotyped or less variable than another species that has a broad range of suction pressure around a similar mean with a CV of 2.0 (CV = st.dev/mean). Thus, rigorous tests for variability in a behavior can be conducted without referring to means enabling comparisons regarding relative stereotypy and the opposite behavior, generalization, to be made.

In contrast, flexibility is a measure of the ability to alter a behavior (suction vs. bite) when the stimulus or treatment is changed (i.e. prey type, feeding phase: capture vs. processing) (Ferry-Graham et al. 2002; Wainwright et al. 2008). Processing events are typically longer than capture and transport (swallowing) events due the need to reduce or reposition the prey rather than simply to move the prey into the mouth or esophagus (Gillis and Lauder 1994, 1995; Motta 2004). Comparing the ability to alter capture or processing behaviors while feeding on the same or different prey types will test relative levels of flexibility. Flexible behaviors can enhance feeding success and permit a broader variety of prey to be taken. On the other hand, when preferred prey is plentiful, non-flexible behaviors are not limiting. Whether species capture and process prey using the same or different mechanisms will allow inferences to be made about ecological niche, particularly when diet is known, which is not often the case for chondrichthyan species.

Several levels of specialist and generalist behaviors have been described in the literature (for reviews see Ferry-Graham et al. 2002; Wainwright et al. 2008). An ecological specialist is ecologically constrained to utilize a narrow range of available resources and is realized when constrained by predatory or competitive interactions (Ferry-Graham et al. 2002), which can only be assessed by dietary and prey availability studies in chondrichthyans. A mechanistic specialist is mechanically constrained to utilize a narrow range of available resources, functionally when due to morphological or physiological constraint (barracuda with a larger mouth area generates weaker suction pressure than bluegill with smaller mouth areas) and behaviorally when due to ability or choice (choosing to use suction or biting behavior) (Ferry-Graham et al. 2002). Stereotypical behaviors, which can indicate specialization, can be tested by comparing the coefficient of variation (st.dev./mean) while flexibility can be tested using ANOVA's or regression (Ferry-Graham et al. 2002; Wainwright et al. 2008). Several chondrichthyan species have been considered to be behavioral or functional generalists based on feeding behavior, such as little skates *Leucoraja erinacea*, lemon sharks *Negaprion brevirostris*, Atlantic guitarfish *Rhinobatos lentiginosus*, spiny dogfish *Squalus acanthias*, and leopard sharks *Triakis semifasciata*, (Motta et al. 1997; Ferry-Graham 1998; Wilga and Motta 1998a, b; Wilga et al. 2007; Gerry et al. 2008). Other chondrichthyan species are considered to be behavioral or functional specialists like swellsharks *Cephaloscyllium ventriosum*, white-spotted bamboo sharks *Chiloscyllium plagiosum*, nurse sharks *Ginglymostoma cirratum*, horn sharks *Heterodontus francisci*, dusky smoothhounds *Mustelus canis*, lesser electric rays *Narcine brasiliensis*, and bonnethead sharks *Sphyrna tiburo* (Ferry-Graham 1997; Motta et al. 1997; Edmonds et al. 2001; Wilga and Motta 2000; Dean and Motta 2004; Nauwelaerts et al. 2007, 2008; Ramsay and Wilga 2007; Wilga et al. 2007; Wilga and Sanford 2008; Wilga 2010). However, while specialist and generalist behaviors among these species are often compared using means, they are not often compared for variability and flexibility (except see Ferry-Graham et al. 2002; Wainwright et al. 2008), which are powerful tests that can distinguish stereotypical, and maybe specialist, behavior.

In this study, our goal is to test for mechanical stereotypy and flexibility in the feeding kinematics and pressure generated during feeding in three chondrichthyan species: two sharks and one skate. Suction feeding ability in three known suction feeding species is tested for interspecific differences while capture vs. processing is tested to determine behavioral differences. Based on previous studies, we hypothesize that *Chiloscyllium plagiosum* shows functional and behavioral stereotypy (has smaller coefficients of variation and less flexibility) while *Squalus acanthias* and *Leucoraja erinacea* are functional and behavioral generalists (have larger coefficients of variation and greater flexibility). Sometime after the evolutionary split between sharks vs. batoids (skates and rays), the ventral portion of the hyoid apparatus (ceratohyal and basihyal) became disconnected from the more dorsal hyomandibula (which suspends the jaws from the cranium) and became attached to the first pharyngeal arch in skates and rays. This has presumably allowed the mechanism for processing prey to evolve along different paths in batoids compared to sharks (Dean et al. 2005). Batoids use lower jaw and hyoid muscles to process prey, while sharks use the upper jaw and associated muscles to reduce prey (Dean et al. 2005). All three species are ecological generalists with respect to diet, therefore squid prey is used and is either a part of or similar to organisms found in the diet: *Squalus acanthias* feeds on pelagic fishes and squid; *Chiloscyllium plagiosum* feeds on benthic fishes, shrimp, crabs, squid; and *Leucoraja erinacea* feeds on a broad variety of benthic invertebrates and fishes (Compagno 1984).

Materials and methods

Animals

Spiny dogfish, *Squalus acanthias*, *(*mean 81 cm TL, range 76–86 cm TL) and little skates, *Leucoraja erinacea*, (mean 43 cm TL, range 41–46 cm TL) were obtained by trawl from Narragansett Bay. White-spotted bamboo sharks, *Chiloscyllium plagiosum*, (mean 76 cm TL, range 69–76 cm TL) were obtained from SeaWorld of San Diego, CA, USA. The dogfish and skates were housed separately in a 8,896 and 1,344 l circular tanks respectively at 16±1°C with a 12 h–12 h light:dark cycle and maintained on a diet of squid (*Loligo* sp.) and fish (*Menidia menidia* and *Clupea harengus*). The bamboo sharks were housed together in a 1,893 l circular tank at 24.4±1°C with a 12 h–12 h light:dark cycle and maintained on a diet of squid (*Loligo* sp.) and fish (*Menidia menidia*). An individual shark or skate was placed in a 1,344 l circular experimental tank to acclimate for 3 days with food withheld at the appropriate temperature. The shark or skate was anesthetized for surgery with a 0.1 gl^{-1} solution of tricaine methanesulfonate (MS-222), which was diluted to 0.05 gl^{-1} during implantation of the sonometric crystals and pressure transducers. After surgery, the shark or skate was allowed to recover in the experimental tank up to 4 h before feeding behavior was recorded. Pieces of squid cut to one mouth width (mw) size to simulate small prey were fed to the shark or skate until satiation. Larger prey would have interfered with crystal communication and pressure recording. Due to the large number of crystals implanted, two experimental protocols were run on each individual, one protocol on gape and hyoid expansion and the second on gape and pharyngeal expansion and standardized by onset of gape expansion.

Sonomicrometry

The movement of selected skeletal elements and pressure in the buccal (mouth cavity), hyoid (throat cavity) and pharyngeal (gill cavity) regions were quantified using sonomicrometry and pressure transducers. The kinematics of 11 internal locations on the walls of the buccal, hyoid and pharyngeal cavities was measured using sonometric crystals (Fig. 1). Gape distance was transduced using crystals

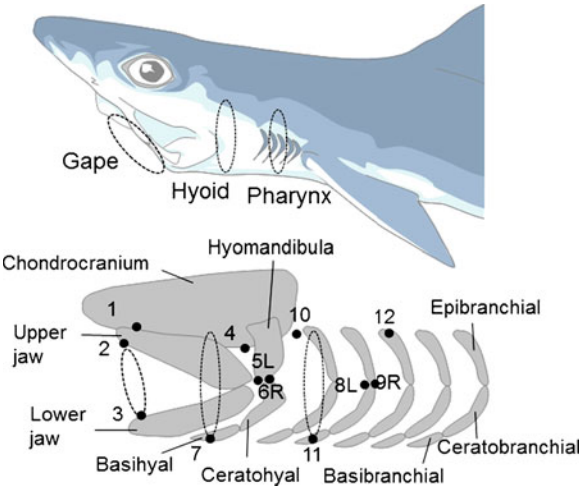

Fig. 1 Lateral view of the dogfish shark (*top*) and skeletal elements (*bottom*). Gape, hyoid and pharyngeal areas are indicated by dashed circles. Dots and numbers indicated crystal placement

2 and 3. Upper jaw protrusion was transduced using crystals 1 and 2. Gape area was calculated based on an expanding circle, verified by video recordings, using gape distance. Hyoid area was calculated using hyoid lateral width and hyoid vertical depression measurements. Hyoid lateral width was transduced from crystals 5 and 6. Hyoid vertical depression was calculated by using the law of cosines to calculate a vertical distance between crystal 7 and a line formed by crystals 1 and 4. The law of cosines required transducing distances between crystals 7 and 1, 7 and 4, and 1 and 4 (for details, see Sanford and Wainwright 2002). Hyoid area was calculated based on an expanding ellipse using hyoid vertical depression and lateral width expansion. Pharyngeal lateral width (expansion) was transduced from crystals 8 and 9. Pharyngeal vertical depression was calculated in a similar way to hyoid depression using the law of cosines to calculate a vertical distance between crystal 11 and a line formed by crystals 10 (anterior roof of pharynx at arch 1) and 12 (posterior roof of pharynx at arch 3). The law of cosines required transducing distances between crystals 11 and 10, 11 and 12, and 10 and 12. Pharyngeal area was calculated based on an expanding ellipse using pharyngeal vertical depression and lateral width. Gape, hyoid and pharyngeal expansion could not be quantified simultaneously due to the large number of wires and pressure probes that would have filled the orobranchial cavity; therefore, the onset of gape expansion served as the reference to standardize and combine the gape and hyoid experiments (crystals 1–7 implanted) and the gape and pharyngeal experiments (crystals 1–3 and 8–12 implanted).

Crystals used were 2 mm diameter omnidirectional piezoelectric crystals with two suture loops on opposite sides of the crystal perpendicular to the wire (Sonometrics, Ontario, Canada). Both loops were sutured to the skin at each location. The wires from the crystals were separated into two bundles, threaded out through each fifth gill slit and sutured to the skin anterior to the first dorsal fin. The fifth gill slit remains open during most of the feeding cycle (Dolce 2009). The sharks did not appear to be bothered by the wires running through the fifth gill slit; they ate readily and ventilated normally during the experiments.

The kinematics of gape–hyoid and gape–pharyngeal expansion was recorded using a 16 channel digital sonomicrometer (Sonometrics) with resolution enhancement to 0.015 mm. SonoVIEW software (Sonometrics) was used to record sonometric data of feeding sharks at a sampling rate of 409.16 Hz and transmit pulse of 250 ns with an inhibit delay of 3.44 µs and 4.57 mm. The distance between selected pairs of crystals was transduced in SonoVIEW and exported to SigmaPlot (Jandel CA USA) for graphing; Excel (Microsoft WA USA) was used to calculate the variables not directly transduced. Variables analyzed include: time to peak area and peak pressure and magnitude of area and pressure for gape, hyoid and pharyngeal regions. The time of peak gape height was set as time zero for reference to other variables.

Pressure

Pressure was recorded simultaneously with sonomicrometry using two Millar SPR-799 microcatheter side-tipped pressure transducers. The pressure transducers were threaded through a plastic cannula, then inserted through the fifth gill slit and fixed to the skin by suture. The gape transducer was sutured on the roof at the midline in the buccal cavity just behind the teeth in *C. plagiosum* and *S. acanthias*. The placement of the jaws facing the cranium prevented implantation of a gape transducer in *L. erinacea*. The hyoid transducer was sutured to the roof at the midline of the cranium between the hyomandibulae while the pharyngeal transducer was placed similarly between the epipharyngeal cartilages of the second branchial arch. The pressure probes were connected to an analog channel on the sonomicrometry system for precise synchronization of pressure and kinematic data. Pressure recordings were analyzed using SonoVIEW for the time and magnitude of pressure relative to ambient for the buccal, hyoid and pharyngeal cavities.

Statistical analysis

Means and coefficients of variation, *T*-Tests and ANOVA's were used to test for stereotypy and flexibility among kinematic and pressure variables by species (*C. plagiosum*, *S. acanthias* and *L. erinacea*) and event (capture and processing). Coefficients of variation using all of the capture and processing events per individual were calculated for each individual as the standard deviation for each individual divided by the mean of each individual. Thus each individual had one coefficient of variation value that was used in the statistical tests. Coefficients of variation were calculated and compared by species and capture vs. processing to determine how variation changes by species and event. Statistical tests (Normality, Homogenous Variances, *T*-Tests, ANOVA) were calculated using SigmaStat (Version 11.0; Systat Software Inc., CA, USA). Students *T*-Tests and One Way ANOVA for normally distributed homogenous data or Mann-Whitney Rank Sum *T*-tests and Kruskall-Wallace One Way ANOVA on Ranks when data could not be transformed to normal.

Results

A total of 303 feeding sequences were analyzed from four *C. plagiosum*, five *S. acanthias* and five *L. erinacea* individuals. Captures were by suction and processing events involved either suction or compression. The number of suction and compression processing events analyzed per species were nearly similar (49, 60, 55% suction events *C. plagiosum*, *S. acanthias* and *L. erinacea* respectively). Descriptive statistics calculated by species (*C. plagiosum*, *S. acanthias* and *L. erinacea*) and behavior (40, 36, and 37 capture events respectively; and 75, 40, and 75 suction and bite processing events respectively) are in Tables 1 and 2. Some processing behaviors were comprised of many individual suction and compressive events while others had only a few, therefore the timing of an individual event may differ among the feeding trials, however, prey transport events were not used. Statistical results for the coefficients of variation on species (capture and processing events combined) and behaviors (species combined) are in Tables 3 and 4.

There are interspecific differences in the magnitude and timing of pressure and area change among the three species (Table 1, asterisks on Figs. 2 and 3). *Chiloscyllium plagiosum* generates lower pressure in all three regions than *S. acanthias* and *L. erinacea*. *Squalus acanthias* has a larger percent change in oropharyngeal (gape, hyoid and pharynx) area than *L. erinacea*, however *C. plagiosum* has a similar change in the hyoid. *Chiloscyllium plagiosum* has shorter times to peak pressure in all regions than *S. acanthias* and *L. erinacea*. Finally, *Squalus acanthias* has shorter times to peak area change than *L. erinacea* and *C. plagiosum*.

Similarly, capture and processing events differ in virtually all variables (Table 2, asterisks on Figs. 4 and 5). Capture events have lower pressures in the gape and hyoid regions than processing events but have larger changes in area. The time to peak pressure and area change is less in capture events than for processing events except for the time to peak area change in the pharynx.

There are also interspecific differences in the coefficients of variation among the three species indicating less variation, or more stereotypy in one or two of the species compared to the others as seen in plots (Table 3, S on Figs. 2 and 3). *Squalus acanthias* has less variation in hyoid pressure change than *C. plagiosum* and *L. erinacea*. *Chiloscyllium plagiosum* and *S. acanthias* have less variation than *L. erinacea* in the magnitude of hyoid area change, while only *S. acanthias* showed less variation in the magnitude of pharyngeal area change. *Squalus acanthias* shows less variation in the time to peak pressure and area change than *C. plagiosum* and *L. erinacea* in all variables except time to peak gape pressure. However, *L. erinacea* also has less variation in time to peak pharyngeal area.

Capture events have less variation than processing events in all variables as shown in the plots of coefficients of variation (Table 4, S on Figs. 4 and 5). Suction processing events have less variation than

Table 1 Statistics for kinematic and pressure variables by species

Variable	*Chiloscyllium plagiosum (C)*	*Squalus acanthias* (S)	*Leucoraja erinacea (L)*	ANOVA or *T*-Test	
	Mean	Mean	Mean	*P*-value	MCT
GA Pressure (kPa)	−8.10	−1.64	–	<0.001	S-C
HA Pressure (kPa)	−10.48	−3.46	−1.21	<0.001	LS-CS
PA Pressure (kPa)	−3.80	−1.63	−0.89	0.007	LS-C
GA% change	3.00	4.75	2.90	<0.001	SC-CL
HA% change	2.23	2.85	1.05	0.007	SC-L
PA% change	1.03	2.42	1.41	0.001	S-CL
GA TTPP (ms)	66.90	85.34	–	0.005	S-C
HA TTPP (ms)	68.01	87.75	78.88	0.015	S-CL
PA TTPP (ms)	57.66	76.20	71.97	<0.001	SL-CL
GA TTP% (ms)	207.08	135.88	279.37	<0.001	L-SC
HA TTP% (ms)	163.41	159.91	325.62	<0.001	L-SC
PA TTP% (ms)	180.86	166.92	203.95	0.005	LS-CS

Species values consist of mean values with capture and processing events combined; *GA* gape area; *HA* hyoid area; *MCT* multiple comparison test result; *PA* pharyngeal area; *TTPP* time to peak pressure; *TTP%* time to peak% change

compressive processing in pressure. Gape area change is similar between the two processing behaviors, but hyoid and pharyngeal area changes are less variable in compressive events. The only duration events that differ in variability are pharyngeal pressure, hyoid and pharyngeal area, which are less variable in suction events.

Discussion

Several instances of mechanical stereotypy as well as flexibility were found in the feeding behavior of the three chondrichthyan species. While the three species differ mechanically in several aspects of kinematics and pressure, *Squalus acanthias* shows more stereo-

Table 2 Statistics for kinematic and pressure variables by behavior

Variable	Capture events Mean	Processing events Mean	*T*-Test *P*-value	Suction processing Mean	Compression processing Mean	*T*-Test *P*-value
GA Pressure (kPa)	−12.55	−1.27	<0.001	−7.94	6.53	<0.001
HA Pressure (kPa)	−7.43	−2.27	<0.001	−6.67	2.80	<0.001
PA Pressure (kPa)	−5.18	−0.47	<0.001	−5.20	5.12	<0.001
GA% change	3.90	3.08	<0.001	3.72	2.34	0.012
HA% change	3.32	1.11	<0.001	2.35	−0.40	<0.001
PA% change	2.63	0.76	<0.001	1.77	−0.56	<0.001
GA TTPP (ms)	44.65	92.37	<0.001	72.87	115.19	<0.001
HA TTPP (ms)	42.11	98.11	<0.001	58.22	145.99	<0.001
PA TTPP (ms)	41.33	83.58	<0.001	60.20	110.70	<0.001
GA TTP% (ms)	77.43	298.32	<0.001	146.94	477.53	<0.001
HA TTP% (ms)	127.06	278.59	<0.001	226.16	339.00	<0.001
PA TTP% (ms)	142.89	212.64	0.076	154.09	284.36	0.005

Behavior values consist of mean values with species events combined. *GA* gape area; *HA* hyoid area; *PA* pharyngeal area; *TTPP* time to peak pressure; *TTP%* time to peak% change

Table 3 Coefficients of variation for kinematic and pressure variables by species

Variable	*Chiloscyllium plagiosum* CV	*Squalus acanthias* CV	*Leucoraja erinacea* CV	ANOVA or *T*-Test *P*-value	MCT
GA Pressure (kPa)	−1.92	−1.75	–	0.774	
HA Pressure (kPa)	−1.64	−0.76	−2.20	0.037	LC-CS
PA Pressure (kPa)	2.05	−1.66	1.84	0.870	
GA% change	0.73	0.85	1.93	0.135	
HA% change	1.15	1.05	2.49	0.003	L-CS
PA% change	1.75	0.75	1.13	0.041	CL-LS
GA TTPP (ms)	0.64	0.49	–	0.730	
HA TTPP (ms)	0.81	0.20	0.88	0.022	CL-S
PA TTPP (ms)	0.78	0.45	0.79	0.035	CL-S
GA TTP% (ms)	1.31	0.59	0.89	<0.001	C-LS
HA TTP% (ms)	0.82	0.44	0.81	0.030	CL-S
PA TTP% (ms)	0.94	0.44	0.52	0.009	C-LS

CV coefficient of variation; *MCT* multiple comparison test result; *TTPP* time to peak pressure; *TTP%* time to peak% change

typed feeding behavior than *C. plagiosum* and *L. erinacea* when feeding on pieces of squid. *Squalus acanthias* exhibits functional stereotypy, while *C. plagiosum* is a functional generalist; however, both species exhibit behavioral flexibility partially supporting the hypotheses. The hypothesis that *Leucoraja erinacea* is a functional and behavioral generalist is supported. Capture events are more stereotyped and show less flexibility than processing events. Conclusions regarding stereotypical behavior using coefficients of variation may not agree with similar determinations using means. Thus, an assessment of the relative level of variation as well as the mean is more appropriate when testing for stereotypical behaviors and making assessments of whether a behavior can be considered specialist.

Species coefficient of variance and means

In general, *Squalus acanthias* shows more stereotyped feeding behavior (smaller coefficients of variation) than *C. plagiosum* and *L. erinacea* when feeding on

Table 4 Coefficients of variation for kinematic and pressure variables by behavior

Variable	Capture CV	Processing CV	*T*-Test *P*-value	Suction processing CV	Compression processing CV	*T*-Test *P*-value
GA Pressure (kPa)	−0.52	−10.11	<0.001	−0.71	0.71	<0.001
HA Pressure (kPa)	−0.63	−3.73	<0.001	−0.80	0.69	<0.001
PA Pressure (kPa)	−0.38	75.04	<0.001	−0.69	0.58	<0.001
GA% change	0.54	1.23	<0.001	1.10	0.85	0.505
HA% change	0.60	1.45	<0.001	0.89	−0.91	0.002
PA% change	0.38	−20.33	0.003	1.04	−1.07	<0.001
GA TTPP (ms)	0.21	0.55	<0.001	0.37	0.52	0.226
HA TTPP (ms)	0.29	0.72	<0.001	0.45	0.47	0.843
PA TTPP (ms)	0.29	0.57	<0.001	0.26	0.47	0.022
GA TTP% (ms)	0.34	0.82	<0.001	0.59	0.52	0.514
HA TTP% (ms)	0.29	0.66	<0.001	0.38	0.64	0.012
PA TTP% (ms)	0.17	0.69	0.003	0.45	0.68	0.049

CV coefficient of variation; *MCT* multiple comparison test result; *TTPP* time to peak pressure; *TTP%* time to peak% change

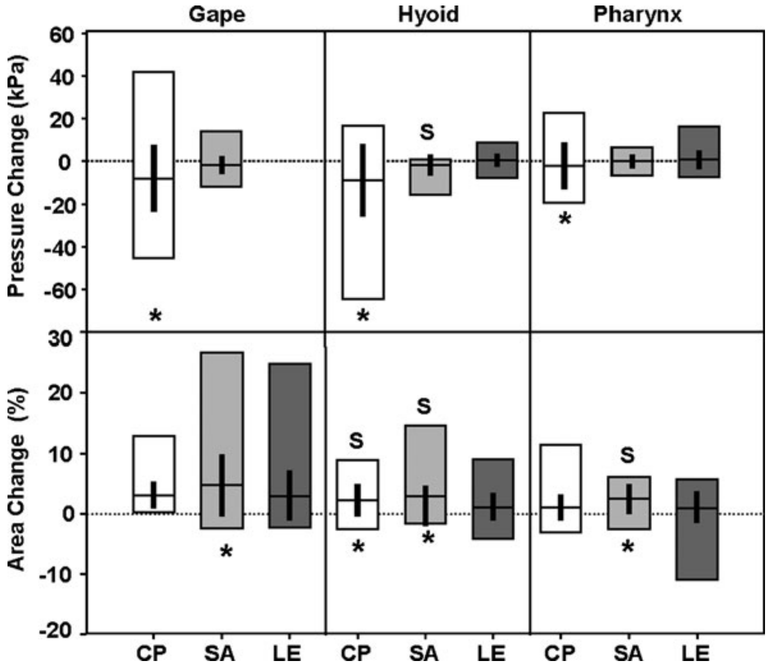

Fig. 2 Plot of pressure and area change by species. CP, *Chiloscyllium plagiosum*; LE, *Leucoraja erinacea*; SA, *Squalus acanthias*. S, indicates stereotyped variable based on coefficient of variation; * indicates significant difference in means

squid pieces. *Squalus acanthias* and *Leucoraja erinacea* used more stereotyped behaviors and more synchronous jaw muscle activity of the left and right sides when feeding on pieces of herring compared to whole herring (Wilga and Motta 1998a; Wilga et al. 2007; Gerry et al. 2008, 2010). Thus, when offered disparate prey types, *S. acanthias* and *L. erinacea* are able to distinguish among prey items and modify muscle activity accordingly, however, whether the kinematics differ remains to be tested. In contrast, *C. plagiosum* and *L. erinacea* have larger coefficients of variation and thus have greater variability in oropharyngeal pressure and kinematics when feeding on squid pieces, which is more typical of generalists.

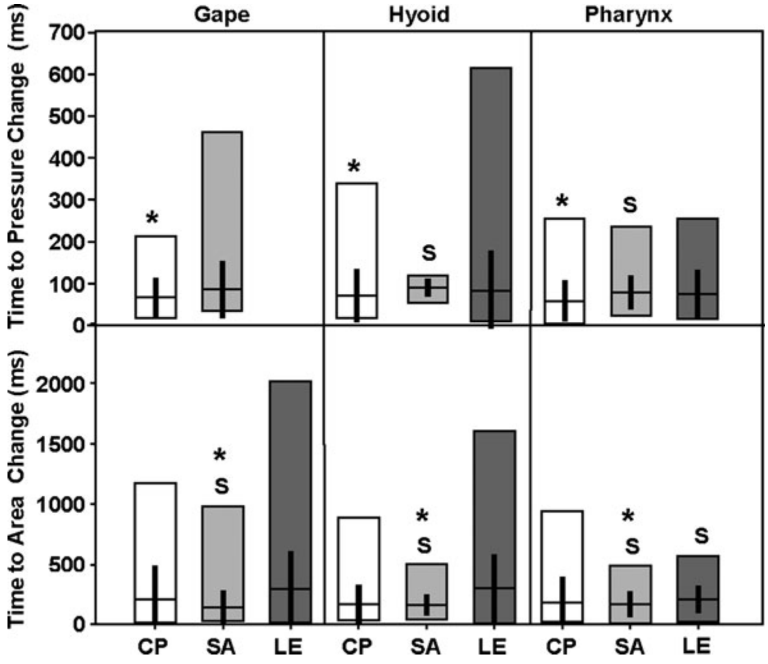

Fig. 3 Plot of time to peak pressure and area change by species. CP, *Chiloscyllium plagiosum*; LE, *Leucoraja erinacea*; SA, *Squalus acanthias*. S, indicates stereotyped variable based on coefficient of variation; * indicates significant difference in means

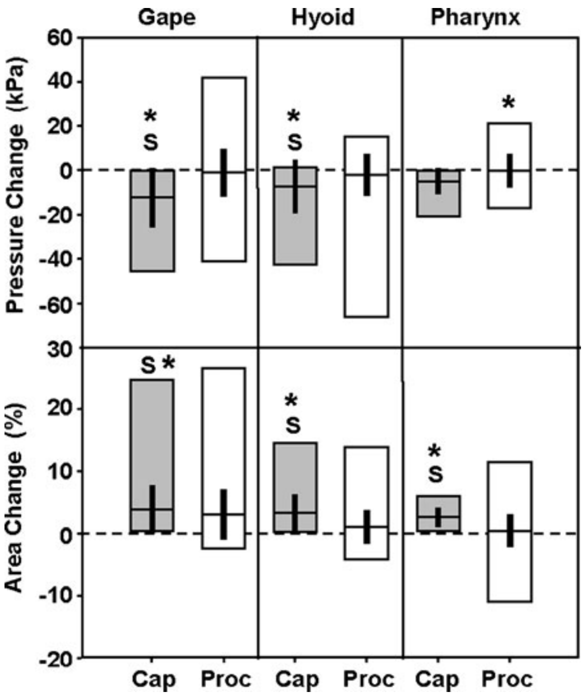

Fig. 4 Plot of pressure and area change by behavior. CP, *Chiloscyllium plagiosum*; LE, *Leucoraja erinacea*; SA, *Squalus acanthias*. S, indicates stereotyped variable based on coefficient of variation; * indicates significant difference in means

However, *Chiloscyllium plagiosum* did not switch to asynchronous jaw muscle activity when feeding on larger more complex prey (Gerry et al. 2008, 2010). The lack of modulation of jaw muscle activity in *C. plagiosum* was attributed to suction feeding being a rapid stereotyped behavior (Gerry et al. 2008); however, the duration and magnitude of suction feeding behavior can be varied broadly as shown here by the results of *S. acanthias* and *L. erinacea*. Thus, conclusions of stereotypy based on how variable a behavior is may differ from that based on means.

Different aspects of feeding behavior stand out among the three species. *Chiloscyllium plagiosum* generates the lowest pressures with the shortest duration in the oropharyngeal cavities. This is primarily why *C. plagiosum* is considered a suction feeding specialist in the literature; pressures as low as −99 kPa have been recorded (Wilga et al. 2007; Ramsay and Wilga 2007; Wilga and Sanford 2008; Gerry et al. 2008). However, the large standard deviation divided by a relatively small mean results in a CV that is relatively large, thus the conclusion that *C. plagiosum* is a suction generalist rather than a suction specialist. In contrast, *S. acanthias* achieves the largest area changes with moderate durations in in the oropharyngeal cavities. *Squalus acanthias* take relatively large whole herring and squid and swallow them whole (Wilga and Motta 1998a). Thus creating a large oropharyngeal area for relatively large prey appears to be more important to successful feeding behavior than generating lower pressures. *Leucoraja erinacea* has smaller oropharyngeal area changes over longer durations, which precludes large pressure changes but may reduce the intake of indigestible material when grasping prey from sandy substrates. *Leucoraja erinacea* also uses asynchronous jaw muscle activity to capture and process prey (Gerry et al. 2008, 2010), which may make decision making a longer process.

Behavior coefficient of variance and means

Capture events are more stereotyped and less flexible than processing events. For capture events, this may be due to the small size of the prey. The best behavior

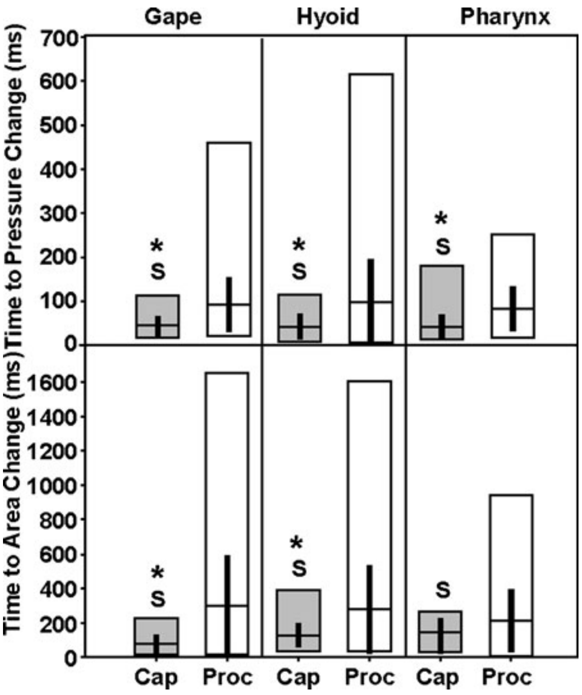

Fig. 5 Plot of time to peak pressure and area change by behavior. CP, *Chiloscyllium plagiosum*; LE, *Leucoraja erinacea*; SA, *Squalus acanthias*. S, indicates stereotyped variable based on coefficient of variation; * indicates significant difference in means

to capture pieces of squid appears to be suction; therefore the change in gape and hyoid area must be fast enough to ensure adequate suction (Lauder and Shaffer 1993), resulting in more stereotyped mechanics. The only variable that does not differ between capture and processing is the time to peak pharyngeal change. The pharynx appears to function as a sink to receive incoming water from the mouth and expel excess water through the gill slits (Wilga and Sanford 2008); therefore it is not surprising that the pharynx dampens flow similarly during both behaviors.

In contrast, processing events are more flexible than capture events. Capture events involved positive changes in oropharyngeal area that typically involved low to moderate levels of suction although some events had low compressive pressure. Processing events involved positive and negative changes in hyoid and pharyngeal area relative to onset (gape area was always positive) resulting in a much broader range of positive and negative pressure changes in all three species. Thus, processing events are more flexible in having more compressive events than capture events even on such simple prey as squid pieces. Processing can then be defined as behaviorally flexible, the ability to use a wide range of suction and compression behaviors to process the same food item, while capture is behaviorally stereotyped in using a narrow range of suction behaviors (Ferry-Graham et al. 2002; Wainwright et al. 2008). Processing events are typically longer than capture and transport (swallowing) events due the need to reduce or reposition the prey rather than simply to move the prey into the mouth or esophagus as has been found throughout aquatic feeding vertebrates (Gillis and Lauder 1994, 1995; Wilga and Motta 1998a, b; Motta and Wilga 2001; Motta 2004).

Suction and compressive processing events were then compared to see where the variation in processing behavior lies. Suction processing events appear to be more stereotypical in the generation of pressure compared to compressive processing events, but this is entirely due to the mean negative pressure of suction events. When the standard deviation is divided by the absolute value for suction, there is no difference in the coefficients of variation between suction and processing events. This means that that the variation around the mean is similar in the two behaviors, just in two different directions. The same applies to hyoid and pharyngeal area change, they are also similar. The only events that differ in variability between suction and compressive processing events are the duration of pharyngeal pressure, hyoid and pharyngeal area, which are less variable in suction events. This is presumably due to the rapid speed of suction behaviors when drawing fluid from the external environment rather than just pushing water around within the oropharyngeal cavity. Note that changing the means to positive in the analysis of capture versus processing does not change the results; variation is still greater in processing events than in capture events.

Relationship of feeding performance to ecology

As mentioned above, it is difficult to study natural feeding behavior of chondrichthyans in the wild; however functional studies can clarify the mechanisms responsible for some feeding behaviors and offer a better understanding of the behavioral interactions that may exist in the wild. The analyses above were intended to determine whether stereotypy and flexibility exists in the feeding mechanism of three species of chondrichthyans by species and behavior. Next, we attempt to integrate those results with those of others to assess the levels of specialization (functional or behavioral) that may exist in the feeding behaviors of chondrichthyans.

The hypothesis that *S. acanthias* is a functional and behavioral generalist feeder on small squid is only partially supported. Rather, *S. acanthias* is a functional specialist as indicated by consistently using suction capture to take squid prey but shows behavioral flexibility in using suction and compression to process the squid. However, in another study, *Squalus acanthias* used suction-bite behaviors to take large prey and suction to take small prey (Wilga and Motta 1998a; Wilga et al. 2007; Gerry et al. 2010), therefore showing more variation in capture behavior. The use of moderate pressure, combined with labial folds, means that prey can only be taken from the area directly in front of the mouth (Lauder and Shaffer 1993; Motta and Wilga 2001; Wilga et al. 2007). *Squalus acanthias* does not stop prior to capturing prey; therefore there is always some degree of ram, or swimming, to bring the mouth close to the prey for a successful strike. A generalist body morphology combining speed and maneuvering morphologies (Thomson and Simanek 1977; Wilga and Lauder

2004) facilitates the taking of primarily elusive pelagic prey (Compagno 1984; Stehlik 2007). This, combined with stereotyped moderately fast and large oropharyngeal openings enables *S. acanthias* to capture a wide range of fast swimming prey types and sizes. Processing is also enhanced by head shaking using asynchronous activation of jaw muscles and recurved cutting teeth to sever long prey, increasing the length of prey that can be taken (Moss 1977; Wilga and Motta 1998a; Gerry et al. 2008, 2010), thus also showing behavioral flexibility in processing various prey types.

Similarly, the hypothesis that *C. plagiosum* is a functional and behavioral stereotypical feeder on small squid is partially supported. *Chiloscyllium plagiosum* generates the strongest suction at the fastest speed, well earning the title of suction specialist (Ramsay and Wilga 2007; Wilga et al. 2007; Gerry et al. 2008; Wilga and Sanford 2008). However, *C. plagiosum* is functionally a generalist that captures prey with widely variable suction pressure (Wilga and Sanford 2008). *Chiloscyllium plagiosum* also shows behavioral flexibility by taking a wide variety of small benthic prey (Compagno 1984). The relatively small mouth constrained by well-developed labial folds that nearly cover the jaws and teeth at peak gape and hypertrophied jaw muscles (Ramsay and Wilga 2007; Wilga et al. 2007) limit the diet to small prey that can be suctioned into the mouth since grasping is difficult. Orectolobiform sharks, including *C. plagiosum*, are benthic ambush predators that inhabit and take prey from complex reef environments (Moss 1977; Compagno 1984; Devadoss 1986) where strong suction is an advantage. Using suction next to a wall (or substrate) *C. plagiosum* doubles the range that suction is effective, therefore extending the strike distance of a suction feeding predator to the prey (Nauwelaerts et al. 2007). *Ginglymostoma cirratum*, a similar orectolobiform species, is known to stop swimming and shove the head into crevices and holes to suction out prey hiding therein, substantially increasing wall effects (Wilga et al. 2007). Orectolobiform sharks also have a benthic body morphology that facilitates maneuvering around complex environments including stopping on the substrate, and walking forward and backwards using enlarged pectoral and pelvic fins on the substrate (Thomson and Simanek 1977; Pridmore 1995; Wilga and Lauder 2004). Tooth function in *C. plagiosum*, and presumably most orectolobiform species except *Orectolobus*, has an inherent functional novelty that increases behavioral flexibility by increasing the available prey types that can be eaten (Ramsay and Wilga 2007). The teeth are normally used to clutch soft bodied prey taken into the mouth by suction, but contact with hard prey pushes the tooth over such that the broad face of overlapping teeth can be used for crushing (Ramsay and Wilga 2007), which increases functional flexibility.

Finally, our hypothesis that *Leucoraja erinacea* is a functional and behavioral generalist is supported. *Leucoraja erinacea* has large coefficients of variation and modulates feeding behavior, which is typical of generalists. Benthic prey is grasped in the jaws assisted by relatively weak pressure. However, the large gape, unhindered by labial folds with flexible timing allows taking larger sized prey from sandy to rocky substrates. Skates are benthic ambush predators that probe the substrate for prey after striking and trapping the prey against the substrate with body and fins (Wilga and Motta 1998a; Wilga et al. in review); therefore rapid jaw movements and suction are not as crucial. The dorsoventrally flattened benthic body morphology with enlarged pectoral fins increases maneuverability and facilitates taking a wide range of prey from the substrate (Compagno 1984; Wilga and Lauder 2004). The large negative changes in the hyoid and pharynx are used to generate compressive pressure for repositioning prey, removing unwanted items, such as carapace pieces, blowing out sand and other indigestible parts (personal observations; Gerry et al. 2008, 2010). Coupled with small multi-cusped teeth and the use of asynchronous jaw muscle activity to further process prey (Gerry et al. 2008, 2010), behavioral flexibility is increased.

In summary, using functional morphology to test for mechanical specializations and flexibility in the feeding mechanics of three suction feeding chondrichthyan species has allowed a more complete understanding of interspecific differences when feeding on a specific prey type (Ferry-Graham et al. 2002; Wainwright et al. 2008). Moreover, these innovative techniques in studying captive shark and skate feeding behavior have clarified the mechanisms responsible for the ecological interactions of capture and processing behaviors, particularly in regards to specialization, although not always as predicted. Thus, these kinds of studies have great potential to better understand the functional and behavioral interactions underlying natural feeding ecology, particularly in species where natural feeding behavior is difficult or impossible to record in the appropriate detail. However, analyses including coefficients of variation as well means are necessary to understand how behaviors differ in variability and flexibility to better understand the interrelationships of mechanics, function, and ecology.

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