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Size does matter – Intraspecific variation of feeding mechanics in the crested newt *Triturus dobrogicus* (Kiritzescu, 1903)

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Abstract: *Many studies have yet been conducted on suction feeding in aquatic salamander species. Within the Salamandridae, the crested newt *Triturus dobrogicus* (Kiritzescu, 1903), occurring from the Austrian Danube floodplains to the Danube Delta, was not subject of investigations so far. The present study examines the kinematics of aquatic suction feeding in this species by means of high-speed videography. Recordings of five individuals of different size and sex while feeding on bloodworms were conducted, in order to identify potential discrepancies among individuals and sizes. Five coordinate points were digitized from recordings of prey capture and twelve time- and velocity-determined variables were evaluated. All specimens follow a typical inertial suction feeding process, where rapid hyoid depression expands the buccal cavity. Generated negative pressure within the buccal cavity causes influx of water along with the prey item into the mouth. Results demonstrate higher distance values and angles for gape in individuals with smaller size. In addition, hyoid depression is maximized in smaller individuals. While *Triturus dobrogicus* resembles a typical inertial suction feeder in its functional morphology, intraspecific differences could be found regarding the correlation of different feeding patterns and body size.*

Keywords: *Amphibians, Salamandridae, *Triturus*, suction feeding, intraspecific variation*

Introduction

Aquatic feeding is the primitive mode of prey capture in vertebrates, and obviously, the physical properties of the medium greatly influence the execution of feeding mechanism [1-4]. The density of water is about 800 times, the viscosity 60 times higher than that of air (depending on temperature, pressure, salinity, etc. [5]), placing constraints on the development of the feeding apparatus, as they limit rapid movements by higher resistance and inertia. Thus, resilient structures withstanding mechanical forces are necessary. Furthermore, the density of prey and water are quite similar, and the predator lunging at the prey induces a bow wave, which pushes the prey away [6]. At the same time, these physical properties of water enable the mechanisms of aquatic prey capture in the first place since the prey is caught in the water current directed towards the predator [7].

Within the Salamandridae three mechanisms of prey capture exist: suction feeding, tongue prehension and jaw prehension [8]. Considering feeding mechanisms, extant salamanders divide into two classes characterized by specializations of the tongue, associated with feeding either in an aquatic or a terrestrial habitat [9]. According to the aforementioned authors, most of the genera are at least partially aquatic, such as those living and feeding aquatically during the breeding season (*Tylotriton*, *Pleurodeles*, *Triturus*, *Neurergus*, *Euproctus*, *Paramesotriton*, *Cynops*, *Hypselotriton*, *Pachytriton*, *Taricha* and *Notophthalmus*), some of them feeding exclusively aquatically (*Pachytriton* and *Pleurodeles*). *Salamandra*, *Chioglossa* and *Salamandrina* possess tongues specialized for terrestrial feeding. Common to all these genera is suction feeding as the exclusive mode of prey capture during their larval stage [10], representing a universal and homologous behaviour pattern amongst this family.

During metamorphosis, aquatic salamanders exhibit different patterns of development. Perennibranchiate species like the Ambystomatidae, Sirenidae and Proteidae, retain a completely larviform habitus, still possessing typical larval features such as external gills, gill slits and posterior branchial elements. On the other hand, completely metamorphosing forms, such as most newts as well as terrestrial and semiaquatic salamanders, lose external gills, gill slits and some posterior branchial elements. Especially, the closing of the gill slits requires a fundamental change in feeding behaviour, a transition from unidirectional to bidirectional suction feeding [11]. Extant water, engulfed along with the prey item, is no longer ejected through the gill slits, but must be expelled through the mouth, in reversed direction to the water stream that transported the prey into the mouth cavity. To some degree, these ontogenetic changes in salamandrid feeding behaviour reflect evolutionary tendencies. Suction feeding is primitive for Osteichthyes, and presumably for Urodeles [4, 12]. Fish employ ram feeding and unidirectional suction feeding, expelling water through the opercular openings. Similarly, larval salamanders capture prey via unidirectional suction feeding and channel extant water through their gill slits. Metamorphosed newts have lost those structures, introducing bidirectional suction feeding, and highly evolved terrestrial feeding taxa like the Plethodontidae undergo a complete reconstruction of the hyobranchial apparatus to enable tongue prehension.

As mentioned above, an aquatic predator utilizes the incompressibility of water for his advantage by rapidly increasing the volume of the buccal cavity. This causes a negative pressure relative to the surrounding water. Since water retains constant volume, a flow is generated, carrying the prey inside the mouth along with the surrounding water [2, 4]. This expansion of the volume is accomplished by rapidly opening the mouth and pulling the hyobranchial apparatus caudoventrally simultaneously. Thus, the hyobranchial apparatus is the main element drawing water inside until the mouth closes again [8].

So, considering feeding a key factor of evolution and identifying the phylogenetic position of Amphibia as a basal lineage of tetrapods, the examination of all behavioural aspects of this clade – especially feeding – is crucial for our understanding of vertebrate evolution and the origin of terrestrial vertebrates. The Danube crested newt *Triturus dobrogicus*, a local aquatic newt of the suborder Salamandroidea, was chosen as subject of this study. Several kinematic variables were used to

describe the feeding kinematics of this species by both comparing kinematic profiles/maximal values of selected movements and quantifying absolute time- and velocity-related values of these movement aspects. This was done to detect behavioural trends and a potential assignability of these trends to either sex or size of the animals.

Materials and Methods

Triturus is a genus within the family of the Salamandridae (true salamanders and newts), which are included in the suborder Salamandroidea (advanced salamanders). For more detailed and most recent information on amphibian systematics and salamander classification, see [13].

The crested newt *Triturus dobrogicus* (Kiritzescu, 1903) along with *Triturus cristatus*, *Triturus carnifex* and *Triturus karelinii* belongs to the *Triturus cristatus* species complex [14-17]. They are widespread in Europe, but declining severely in their distribution areas [18]. The conservation status of *Triturus dobrogicus*, which occurs from the Austrian Danube floodplains and the Pannonia lowlands to the Danube delta, is considered “near threatened” (<http://www.iucnredlist.org/details/22216/0>). Populations of this species are increasingly isolated and their size is decreasing due to loss of habitats by conversion of small temporary water bodies and wetland into arable cropland [18-20]. Other natural environments like Danube river branches with low velocity are disappearing gradually due to stream regulation and soil sealing.

Triturus dobrogicus is a small, narrow headed newt with short, slender legs. The total length in males averages 14 cm and in females up to 17 cm. The skin on the back and the sides is covered with numerous small warts. The dorsal coloration is brown to black, the belly is usually yellow to bright orange with many, sharply defined, black patches. Many small white spots appear on the sides and on the throat, which is mostly black. The tail takes up to half of the total length. When reaching sexual maturity after more than two years [21], males develop a characteristic dorsal comb with an irregular jagged edge. The crest is pronounced during the breeding season, the shape of the jags change from finger-shaped to irregular over the course of the life, and are an indication of age [22]. Instead of a crest, females frequently show a dorsal brown line, which is also visible in young animals.

Five specimens (two males, three females; see Table 1 for measurements) of *Triturus dobrogicus* - purchased from a local breeder - were studied. The animals were accommodated in an aquarium (100 x 40 x 40 cm, water level about 30 cm, ambient water temperature and 12h/12h day-night photoperiod), which was equipped with roots, moss and floating driftwood.

Table 1: Length and weight measurements of the investigated specimens of *Triturus dobrogicus*. Working names include size and sex.

Working names	Length (mm)	Weight (g)
Large female (LF)	152	11.95
Intermediate female (IF)	144	10.05
Small female (SF)	133	6.4
Large male (LM)	121	5.2
Small male (SM)	108	3.6

In order to record the feeding process, a high-speed camera (Photron FASTCAM, 1024PCI, San Diego, USA) and according control software (Photron FASTCAM Viewer, v3600_64bit, San Diego, USA) were used. The camera was equipped with a Nikon Makro objective (Nikon AF D 24-85/2.8-4IF, Nikon Corporation, Tokyo, Japan). Illumination of the film set was created via usage of two Dedocool Lights (Dedo Weigert Film GmbH, Munich, Germany). The films were recorded in a glass cuvette (30 x 10 x 20 cm) half-full of water, at 1000 frames per second with a resolution of 512 x 256 pixel. For adaptation to the high illumination during filming, specimens were exclusively fed within the filming cuvette. For this purpose, the animals were isolated from each other during feeding. The

specimens were fed every third day with bloodworms (Chironomidae) of about 1 cm length. The prey was placed on the bottom of the filming aquarium in front of the animals in order to ensure similar results concerning perspective of filming. The animals were consistently filmed in lateral view. Overall, 86 videos were recorded and the best five - meaning lateral view for the complete food uptake process - of each individual were selected. The sample size was chosen according to similar studies on feeding kinematics [e.g. 23-25]. For analysis of recordings, five landmarks were defined and tracked frame-by-frame using a digitalization program by Christian Beisser implemented in MATLAB (MATLAB R 2015b, MathWorks, Inc. Natick, MA, USA), which is based on a point tracking algorithm by Ty Hedrick [26]. The landmarks used include the tip of the lower and upper jaw, posterior end of the prey, mouth corner and posterior tip of the hyobranchial apparatus (joint between the first epibranchial and first ceratobranchial; Fig. 1).

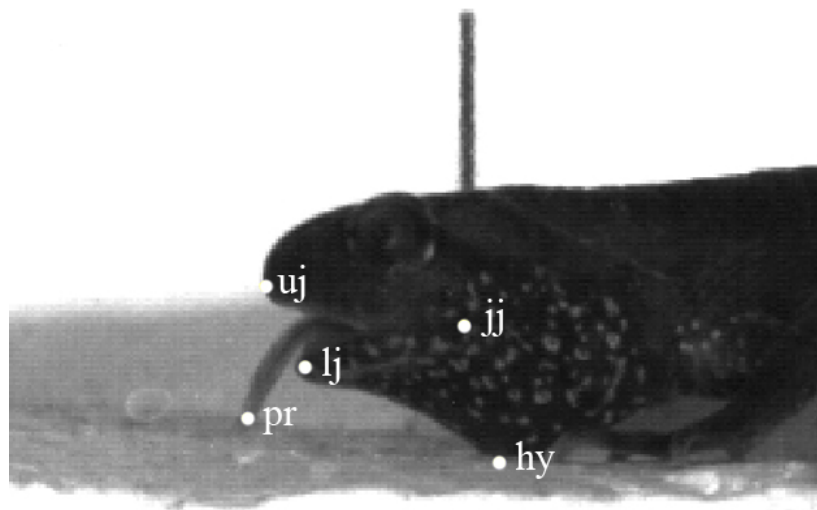


Figure 1: Landmarks of the kinematic analyses on *Triturus dobrogicus*. uj – upper jaw, lj – lower jaw, jj – jaw joint, hy – hyobranchial apparatus, pr – prey. Line in the background provides information for calibration (1 cm).

Further analyses were made using MATLAB programs (implemented in MATLAB R2015b), which were designed by Christian Beisser and Patrick Lemell and programmed by Christian Beisser. With the aid of these programs, the following kinematic profiles were analysed: jaw movement (distance between the landmarks uj-lj), jaw angle (angle between landmarks uj-jj-lj), hyobranchial depression (distance between hy and jj), and prey movement (distance between pr and uj). From the kinematic profiles, twelve variables were determined: duration of the gape cycle (time from beginning of mouth opening until closing of the mouth), duration of mouth opening (beginning of mouth opening to maximum gape), duration of gape plateau (max mouth opening until start of mouth closing), duration of mouth closing (maximum gape till mouth closure), velocities of opening and closing, duration and velocity of hyoid depression (beginning of hyoid depression until maximum depression), duration and velocity of prey ingestion (onset of prey motion till prey disappeared inside buccal cavity), time interval between start of mouth opening and start of hyoid depression, time interval between maximum gape and maximum hyoid depression.

Results

In the analysed videos, all specimen approached the prey and used suction feeding by rapidly opening the mouth followed by hyobranchial depression. This expanded the buccal cavity, thus dropping pressure within the buccal cavity and sucking water and prey into the mouth. For comparison, typical

feeding events for a large and a small specimen are shown in Fig. 2, kinematic profiles of gape and hyoid depression are presented in Fig. 3.

Among the investigated females, the smallest animal showed the widest gape angle with about 40° on average, with considerably low standard deviation. In contrast, the biggest female exhibited a comparatively low gape angle of 15° , the intermediate female resided in between (20°) with considerably higher standard deviations. Also male specimens displayed higher gape angles with decreasing size; the biggest male just opened the mouth to about 12° , whereas the smaller male reached 25° . Similarly to the females, the standard deviation was again higher in the bigger specimen.

Looking at the kinematic profiles, the smallest specimen again showed the most homogenous curves. The large animals showed a much higher variability within their feeding kinematics with regard to gape and hyobranchial depression as well, although the hyobranchial depression seemed to be rather constant for all sizes and both sexes.

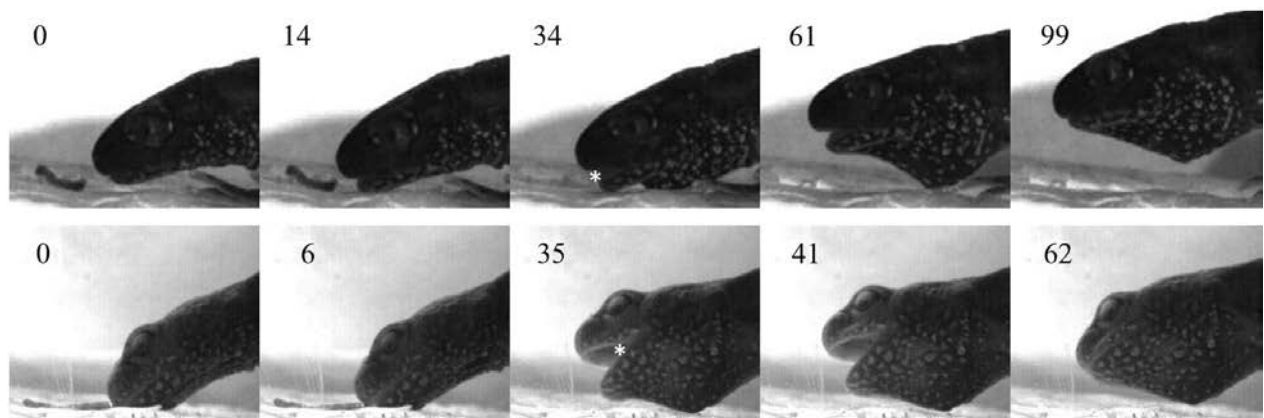


Figure 2: Suction feeding event of *Triturus dobrogicus* showing prey capture. Above five frameshots of the big female, underneath five frameshots of the small female; numbers indicate framenummer as well as time in ms. Selected frames display start of mouth opening, start of hyobranchial depression, maximum gape (prey is indicated by asterisk), maximum hyobranchial depression and mouth finally closed.

Although it is not clearly visible within the profiles of the gape cycle (Fig. 3), there was always a plateau phase distinguishable for all sizes and sexes. Again, there was a tendency for longer duration from larger specimens to smaller ones. Furthermore, the timing of the start of hyobranchial depression after the start of mouth opening tended to be prolonged from smaller to larger subjects and consequently, the maximum depression occurred after the maximum gape was reached (see Table 2).

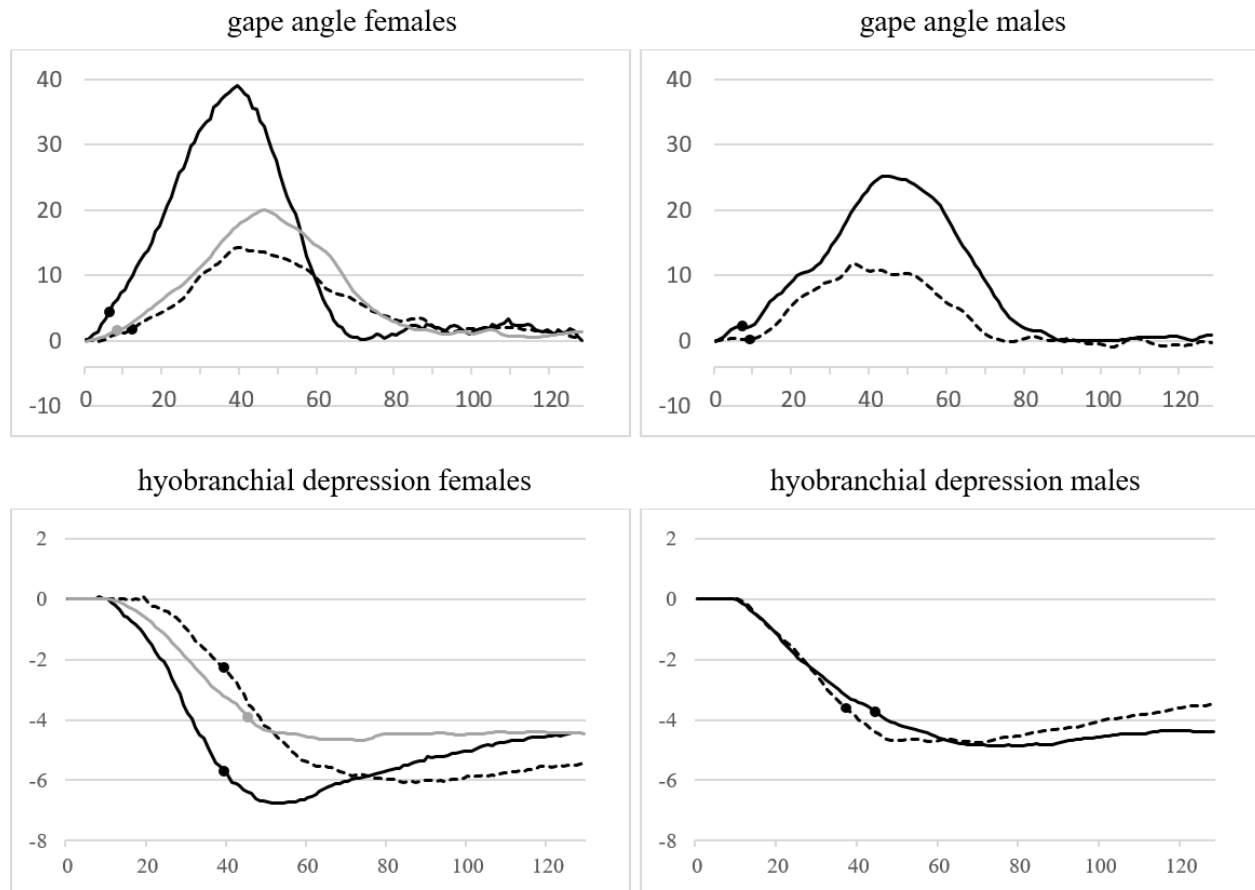


Figure 3: Kinematic profiles of gape angle and hyobranchial depression of females and males. Mean curves of big female (dotted line), intermediate female (grey line) and small female (line) are compared with mean curves of big male (dotted line) and small male (line). Dots on curves represent start of hyobranchial depression on gape curves and timepoint of maximum gape on depression curves. X-axis as framecount, y-axis as degree (angle) and mm (depression).

Table 2: Mean and standard deviation of kinematic variables of feeding in *Triturus dobrogicus*. Durations in ms, velocities in mm/s.

	large female	med. female	small female	large male	small male
kinem. variable	Mean +/- SD	Mean +/- SD	Mean +/- SD	Mean +/- SD	Mean +/- SD
gape cycle	0.074 +/- 0.016	0.087 +/- 0.014	0.068 +/- 0.006	0.074 +/- 0.023	0.083 +/- 0.006
gape opening	0.029 +/- 0.006	0.034 +/- 0.004	0.032 +/- 0.004	0.031 +/- 0.011	0.038 +/- 0.004
mean vel.	75.20 +/- 31.28	94.84 +/- 37.36	144.50 +/- 13.98	68.73 +/- 30.87	94.20 +/- 22.68
plateau	0.019 +/- 0.009	0.016 +/- 0.009	0.009 +/- 0.003	0.015 +/- 0.002	0.011 +/- 0.004
gape closing	0.026 +/- 0.009	0.037 +/- 0.007	0.027 +/- 0.004	0.028 +/- 0.014	0.034 +/- 0.003
mean vel.	75.99 +/- 42.26	90.29 +/- 49.69	168.64 +/- 16.18	69.16 +/- 24.31	102.29 +/- 21.03
hyobranch. depr.	0.044 +/- 0.008	0.038 +/- 0.003	0.034 +/- 0.002	0.041 +/- 0.011	0.046 +/- 0.011
mean vel.	139.05 +/- 18.47	133.66 +/- 9.81	195.06 +/- 29.24	127.12 +/- 64.68	111.89 +/- 34.35
start gape-hyo	0.013 +/- 0.005	0.009 +/- 0.004	0.007 +/- 0.002	0.010 +/- 0.005	0.008 +/- 0.004
max gape-max hyo	0.022 +/- 0.009	0.013 +/- 0.006	0.006 +/- 0.002	0.022 +/- 0.003	0.016 +/- 0.009
attack mean vel.	63.54 +/- 16.31	62.36 +/- 20.43	122.02 +/- 39.07	53.64 +/- 18.74	59.85 +/- 13.42
suction mean vel.	597.92 +/- 169.42	781.54 +/- 278.39	747.20 +/- 364.82	256.96 +/- 85.71	340.45 +/- 244.52

Looking at the kinematic variables in Table 2, several intraspecific differences became obvious. While the durations for the gape cycles were quite uniform, the velocities of opening and closing were much faster with decreasing size of the specimens of same sex. This was quite obvious when correlating the data with the higher gape angle values of the smaller subjects (Fig. 4). Thus, the velocities increased with decreasing size of the animal. For hyobranchial depression, only the smallest female showed any sort of perfect curve shape: a fast depression almost aligned with the gape opening, followed by a slow elevation to bring the hyobranchial apparatus back to its initial position. All other specimens performed their depression in a similar way, but departing from the former mentioned animal (Fig. 3). Comparing the attack speed of *Triturus* on the chironomid larvae, again the smallest female showed twice the values of the other ones. The suction force, measured by the speed of the prey, showed some sexual dimorphism, although standard deviation is quite high in all subjects. Males produced noticeable less suction force than females.

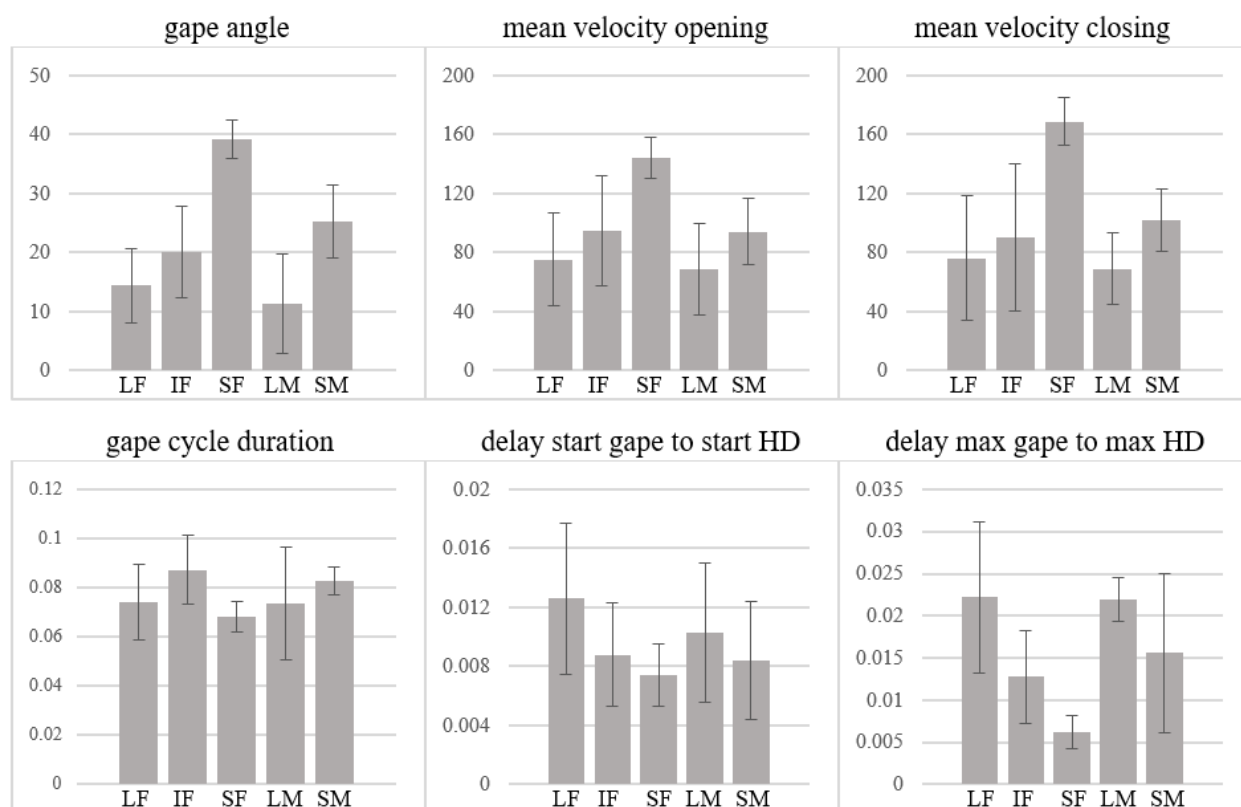


Figure 4: Plots representing special kinematic variables of *Triturus dobrogicus*. Y-axis either in degrees (angle), mm/s (velocities), or ms (durations). HD-hyobranchial depression, LF-large female, IF-intermediate female, SF-small female, LM-large male, SM-small male.

Discussion

Kinematic profile:

All specimens of *Triturus dobrogicus* showed the typical pattern of aquatic suction feeding. They created lower pressure compared to the surrounding medium within the buccal cavity by depression of the hyobranchial apparatus, thus carrying the prey item into the mouth along with a stream of water. In all feeding events, the hyobranchial depression continued beyond the gape cycle, as described for amphibians [27-28] and for other suction feeding taxa like teleosts [12] and turtles [29-30]. The kinematics of prey capture in both salamanders and fish are very similar, as a result of hydrodynamic constraints [31]. The gape cycle is expressed in an almost bell-shaped curve, mouth opening and mouth closing are of almost equal length, which is in concordance with other aquatic feeders within

related salamandrids [24, 32], as well as some ambystomatids [23]. The depression of the hyobranchial apparatus in *Triturus dobrogicus* occurred slightly after the beginning of the gape cycle, in accordance with Deban & Wake [27]. Maximal hyobranchial deflection was reached shortly after maximum gape, representing a kinematic characteristic, shared by many aquatic vertebrates like teleosts [33] and dipnoans [34-35]. Hyobranchial depression occurred in one rapid movement and the duration of this expansive phase was always a multiple times shorter (8-10 times) than the slow and gradual elevation of the hyobranchium, which is similar to other ambystomatids [36]. According to Deban & Wake [27], mouth opening occurs more rapidly than hyobranchial depression, which constitutes the typical pattern of suction feeding. Accordingly, Deban & Marks [37] emphasise the greater velocity of mouth opening, compared to hyobranchial depression in plethodontid salamanders. However, in *Triturus dobrogicus* the depression of the hyoid apparatus was highly accelerated, being markedly faster on average than mouth opening (see Table 2). Hyobranchial depression is mainly responsible for expanding the buccal cavity, thus creating suction. Little is known about the contribution of accelerated mouth opening to a generation of low pressure for suction feeding [24]. Nevertheless, we could observe on several occasions that within one feeding event a minor hyobranchial depression was compensated by a more pronounced gape and vice versa, showing a tendency for both of these aspects of the feeding movement to complement each other. The ability to create low pressure for suction feeding just by an accelerated mouth opening has been reported for the Chinese giant salamander (*Andrias davidianus*; [24]). The modified suction mechanism employed by this species does not rely on hyobranchial depression. Instead, rapid separation of the surfaces, formed by the broad and long upper and lower jaws, is exclusively responsible for the acceleration of the water stream towards the mouth. Hyobranchial depression, occurring after the gape, does not contribute to suction velocity in *Andrias davidianus*. This alternative mode of generating suction is hypothesized to be primitive for salamanders. Although the main propulsive force for acceleration of prey was created by hyobranchial depression in *Triturus dobrogicus*, analyses of the kinematic profiles showed that jaw motion contributed to suction force, at least in the beginning.

Intraspecific variability:

Apart from the sexual dimorphism in *Triturus dobrogicus* regarding body size, no relevant differences were found with respect to its feeding kinematics. Only the mean suction velocity of males is noticeably diverging, although a high standard deviation was present for both sexes. Nevertheless, a high intraspecific variation could be shown regarding size of the individuals. So far, different sized animals were never investigated, apart from differences in feeding kinematics of salamanders before and after metamorphosis. For example, Reilly [38] examined the ontogenetic variability in feeding behaviour in different life stages of *Salamandra salamandra* and Lauder & Shaffer [39] investigated motor pattern conservatism during metamorphosis in the tiger salamander (*Ambystoma tigrinum*) via electromyographic measures of muscle activity. Data presented in Fig. 4 clearly show a sequence from large to small animals regarding gape angle (highest in smaller specimens, lowest in large ones), mean velocities of mouth opening and closing (again highest in smaller specimens). The timely delay of movements of the hyobranchial apparatus with respect to the gape cycle showed intraspecific variations as well – from higher intervals in larger subjects to very short intervals in the smaller ones. Apparently, larger and therefore older specimens simply do not exploit their full potential for each feeding event. They always show higher deviation values, and therefore much higher variability in contrast to the high degree of homogeneity and consistency of the smaller animals. Stereotypy of feeding behaviour is considered the invariance of procedure in prey capture from initiation to completion, and the inability to modulate this behaviour [38]. The research conducted on this issue is vast, still there is no universal terminology, which incorporates the various sources of variability and communicates their biological significance [40]. It seems that the smallest specimens are highly stereotyped in their behaviour, and tend to perform every movement reaching to the limits of their physiological and anatomical capacity. The intensities and the timing of the movement aspects are designed to generate maximum flow of water into the mouth, regardless of necessity and the demands

of the situation in the particular feeding event. They seem not to be able to modify the feeding behaviour according to the actual circumstances. Contrarily, the experience of the larger and therefore older specimens allows them to respond to slightly changed circumstances by varying for example the distance to the prey item before capture. A lateral displacement of the prey as well as an oblique or inclined position of the body, in relation to the prey, are compensated with alterations of behaviour, still resulting in successful prey capture. Furthermore, smaller individuals probably acquire food faster and more voraciously as larger individuals have sufficient energy, and the need to gather food is not as pressing to them.

Conclusions:

Adult specimens of *Triturus dobrogicus* followed a kinematic pattern of suction feeding that conforms to the general pattern defined as being primitive for salamanders [4, 23, 27, 28, 38, 41] and other aquatic vertebrates [12, 29, 33, 35, 42]. However, intraspecific variations were detected. Smaller specimens of both sexes achieved greater gape angles and hyobranchial depression than larger ones. They showed stereotyped feeding patterns in contrast to the larger animals, which was expressed in much higher standard deviations. Furthermore, it seemed that older specimens did not exploit their full potential for each feeding event as the smaller ones do. A stereotyped feeding behaviour has its advantages during ontogeny; the rate of successful prey capture is higher when staying with a proven system. On the other hand, the energy costs are much higher. Larger animals showed more flexibility and variability of their feeding patterns. They were able to respond to various circumstances like prey size or movability. Thereby, energy costs can be reduced to the bare necessities, making these animals even more successful.

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