Broader head, stronger bite: *In vivo* bite forces in European eel *Anguilla anguilla*

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This work examined three different phenotypes of the yellow-eel stage of the European eel *Anguilla anguilla*, broad-heads, narrow-heads and eels with an intermediate head shape. The aim was to see whether broad-headed *A. anguilla*, which generally consume harder, larger prey, such as crustaceans and fish, exerted greater bite force than the narrow-headed variant, which mainly consume soft, small prey such as chironomid larvae. It was found that in 99 yellow *A. anguilla*, *in vivo* bite force of broad-heads are higher compared with narrow-heads and intermediates.

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Foraging performance comprises the ability of an animal to locate, capture, and handle prey, which is a strong determinant of fitness (Wainwright, 1988, 1991). One of the most important performance measures is bite force as it is not only linked to an animal's morphology but also to its dietary ecology (Grant & Grant, 1996; Anderson *et al*., 2008; Herrel & Holanova, 2008). Previous studies have described associations between bite force and dietary ecology, with higher bite forces enabling animals to consume hard and large prey. This has been shown in several fishes such as sharks (Selachimorpha; Kolmann & Huber, 2009; Habegger *et al*., 2012), the spotted ratfish *Hydrolagus colliei* (Lay & Bennet 1839) (Huber *et al*., 2008), the great barracuda *Sphyraena barracuda* (Edwards 1771) (Grubich *et al*., 2008) and piranhas (Characidae; Grubich *et al*., 2012). The generation of higher bite forces is also related to variation in cranial morphology. One of the most common ways to increase bite force is through jaw muscle hypertrophy, which has been demonstrated in certain catfishes (Siluriformes; Herrel *et al*., 2002), finches (van der Meij, 2004), sharks (Huber *et al*., 2006; Habegger *et al*.,

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2012) and lizards (Herrel *et al.*, 2007). Larger jaw muscles are generally associated with larger, broader heads.

Interestingly, in the yellow-eel stage of the European eel *Anguilla anguilla* (L. 1758), two phenotypes have been distinguished related to head width: broad and narrow-head variants (Thurow, 1958). Broad-heads have larger jaw muscles (De Schepper, 2007), which has been linked to dietary preferences, as both stomach contents and stable-isotope analyses showed that broad-heads tend to feed on harder and larger prey, such as crustaceans and fish, whereas narrow-heads generally consume soft, small prey, mainly benthic invertebrates such as chironomid larvae (Lammens & Visser, 1989; Proman & Reynolds, 2000; Cucherousset *et al.*, 2011). The smaller size and softer material properties of prey items consumed by narrow-heads allow these prey to be ingested by suction feeding, whereas the harder and larger prey items of broad-heads require biting behaviour or rotational feeding (Helfman & Winkelman, 1991). It is thus predictable that larger jaw muscles should allow broad-heads to generate higher bite forces, facilitating biting behaviour and rotational feeding. This hypothesis, however, has not been tested yet.

To test this, yellow-stage (*A. anguilla*) were captured during June ($n = 46$), July ($n = 26$), and October ($n = 27$) 2007 in Lake Weerde (50° 58′ ″ N; 04° 28′ 58″ E), Belgium, using electric fishing and fyke nets. Upon capture, pictures of the head were taken in dorsal view and the total length (L_T) was measured. Bite forces were measured using a Kistler type 9203 piezoelectric force (± 500 N) transducer [Kistler Inc.; www .kistler.com;, Switzerland; Fig. 1(a)] mounted in a custom-built holder and connected to a portable Kistler type 5059A charge amplifier (Herrel *et al.*, 1999). The fish were made to bite on the free end of the holder, by which the forces were transferred to the transducer across the fulcrum. Forces were registered with a portable charge amplifier. To standardize for gape angle, the distance between the bite plates was changed for *A. anguilla* of different sizes. The *A. anguilla* were induced to bite at the posterior end of the mouth, which corresponds to the bite position in the wild (J. D. M. pers. obs.). Most *A. anguilla* bit spontaneously on the transducer. In case fish were unwilling to bite, they were stimulated to bite by touching the side of the mouth with a finger, which resulted in the fish biting on the plates. At least two and maximum five independent bite measurements were recorded per specimen, depending on the willingness of each individual. Age and sex of the *A. anguilla* was not determined. After manipulation, all *A. anguilla* were returned unharmed to the lake. Afterwards, head width just posterior to the eye (W_H) and head length (L_H) were measured from the images using imageJ (Schneider *et al.*, 2012). Subsequently, $W_H L_H^{-1}$ was calculated and used as an index of head width. It was noted that in our sample, $W_H L_H^{-1}$ tends to increase with L_T [Fig. 1(b)]. Therefore, the unstandardized residuals of the linear regression between $W_H L_H^{-1}$ and L_T were calculated and the residual values ranked. The 33 specimens with the highest values were considered broad-headed, the 33 specimens with the lowest values narrow-headed and the remaining 33 were treated as intermediates.

The maximum bite force of the different bites was used for further analysis, using the $\log_{10}$ values of L_T and the maximum bite force (F_{Bmax}). While the different morphotypes do not significantly differ in size, there is a considerable variation in size within each group (Table I). Consequently, there might be ontogenetic variation in bite force in the different groups, as was observed in the black piranha *Serrasalmus rhombeus* (L. 1766) (Grubich *et al.*, 2012). To correct for a possible ontogenetic effect, an ANCOVA
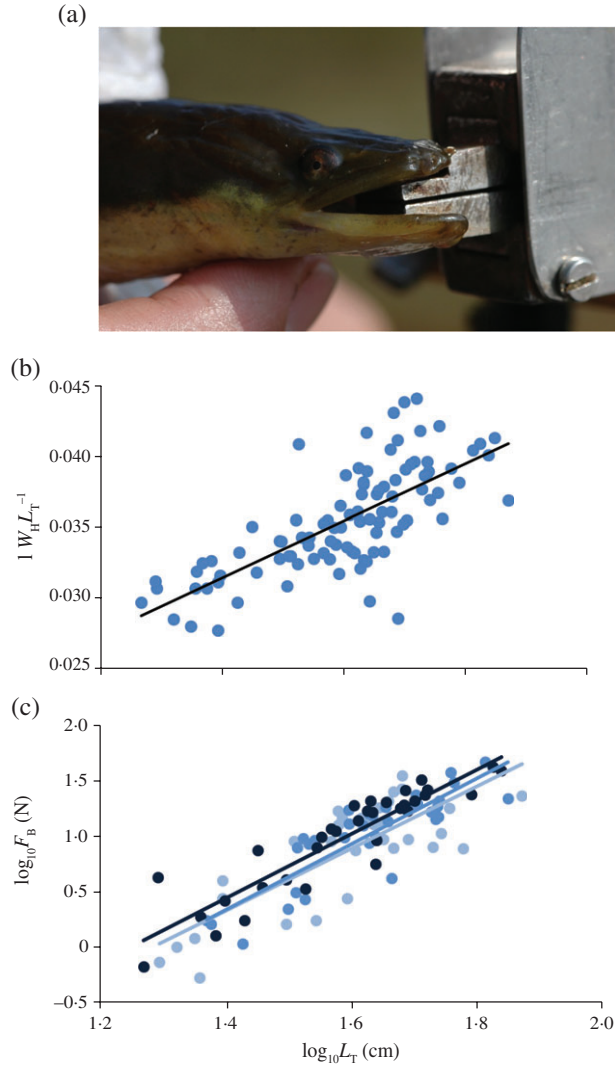
(a)

(b)

(c)

FIG. 1. (a) European eel *Anguilla anguilla* biting on the Kistler piezoelectric force transducer. (b) Relation between head width: and total length ($W_H L_T^{-1}$) and $\log 10(L_T)$; $y = 0.099x + 0.107$, $r^2 = 0.33$, $P < 0.001$. (c) Relation between $\log_{10}$ bite force (F_B) and $\log_{10}(L_T)$ for narrow-heads (—●—, $y = 2.79x + 3.56$, $r^2 = 0.65$, $P < 0.001$), intermediates (—●—, $y = 2.94x + 3.77$, $r^2 = 0.75$, $P < 0.001$) and broad-heads (—●—, $y = 2.88x + 3.58$, $r^2 = 0.83$, $P < 0.001$).

was performed on the $\log_{10} F_{Bmax}$, with $\log_{10} L_T$ as covariate. This identifies significant differences in bite force between the different groups while correcting for body size. The *in vivo* bite forces scale with significant positive allometry in all three groups (slope narrow-heads 2·79; slope intermediates 2·94; broad-heads 2·88; $P < 0.05$). Furthermore, these slopes do not differ significantly between the different groups ($P = L_T$), indicating that the ontogenetic increase in bite force does not differ between the different morphotypes. Subsequently, the ANCOVA indicated that, when comparing eels

TABLE I. The mean $\pm$ S.D. of total length (L_T, cm) and bite force (F_B, N) in narrow-head, intermediate and broad-head morphs of *Anguilla anguilla* and the results of ANCOVA comparisons between head types

	Head shape			Between group comparisons			
	Narrow (NH)	Intermediate (INT)	Broad (BH)	P_{NH-INT}	P_{BH-INT}	P_{BH-NH}	$P_{=L_T}$
$\log_{10}L_T$	$1 \cdot 59 \pm 0 \cdot 14$	$1 \cdot 63 \pm 0 \cdot 12$	$1 \cdot 59 \pm 0 \cdot 15$	$>0 \cdot 05$	$>0 \cdot 05$	$>0 \cdot 05$	–
$\log_{10}F_{Bmax}$	$0 \cdot 895 \pm 0 \cdot 481$	$0 \cdot 938 \pm 0 \cdot 402$	$1 \cdot 026 \pm 0 \cdot 456$	$>0 \cdot 05$	$>0 \cdot 05$	$<0 \cdot 05$	$> 0 \cdot 05$
Residual F_B	$-0 \cdot 058 \pm 0 \cdot 286$	$-0 \cdot 015 \pm 0 \cdot 201$	$0 \cdot 073 \pm 0 \cdot 187$	$>0 \cdot 05$	$>0 \cdot 05$	$<0 \cdot 05$	–

$=L_T$, comparison between fish of equal length.

that are similar in size, broad-heads are able to generate higher bite forces than intermediates and intermediates higher bite force than narrow-heads. The differences in bite force were, however, only significant between broad and narrow-heads (Table I); broad-heads of a similar length as narrow-heads tend to bite harder [Fig. 1(c)].

To confirm the results of the ANCOVA, the unstandardized residuals were calculated for the $\log_{10}F_{Bmax}$ using a linear regression with $\log_{10}L_T$, with positive values representing higher bite forces than expected and negative values lower bite forces than expected for the size of the *A. anguilla*. Since the assumptions for an ANOVA were not met, a non-parametric permutation test (10 000 replicates) was performed to find significant differences between the different groups. This confirmed the results of the ANCOVA, with broad-heads generating significantly higher bite forces than narrow-heads (Table I), but not significantly different from those of intermediates. Also here, narrow-heads had the lowest bite forces. Furthermore, it was seen that 70% of the broad-heads had positive residual values and thus generated higher bite forces than expected for their length, while this was only the case for 54% for intermediates and 52% for narrow-heads.

Still, the variation in bite force when comparing specimens of similar length and head shape is relatively high. There are several possible explanations for this phenomenon. First, it is possible that eels differed in motivation to bite. By repeating trials several times for each animal and then retaining only the maximum force, it increased the probability of measuring the maximum biting capacity of an individual and minimized the effect of motivation. Nevertheless, motivation can be an issue. Second, while variation in gape angle was standardized by increasing or decreasing the distance between the bite plates depending on fish size, it could still be possible that there was slight variation in the position of the jaw where the fish bit. By repeating the trials, however, this effect should have been minimized. Third, variation in the lever mechanism could play a role. Next to head width, variation in head height could, for example, also influence bite force, since higher heads can lengthen the in-lever of jaw adductors (Lappin *et al*., 2006). In addition, De Schepper (2007) showed that broad-heads exhibit longer lower and upper jaws than narrow-heads. Variation in jaw length could, in turn, affect bite force as it influences out-lever length (Westneat, 2003). Fourth, there might be additional variation in the muscular morphology not related to head width and thus muscle size. For example, differences in fibre length and orientation, or in the ratio of slow-twitch *v*. fast-twitch fibres can also have an effect on the measured bite force.

Finally, it is possible that a combination of all or some of these factors affected the observed variation in bite force.

Still, the results here confirm the hypothesis that broad-heads are capable of generating higher bite force than narrow-heads. This can not only facilitate biting behaviour, but also can improve holding grip during rotational feeding. During rotational feeding, *A. anguilla* grab large prey in their mouth and spin along their long axis to tear off smaller pieces (Helfman & Winkelman, 1991). This allows them to omit gape limitation and consume large and hard prey items, such as fish. It can thus be expected that broad-headed *A. anguilla* are capable of dealing more efficiently with such harder, larger prey.

The differences, however, in measured bite force between broad and narrow-heads are not extremely pronounced [Fig. 1(c)], which is interesting since De Schepper (2007) showed that broad-heads are associated with larger jaw muscles. This implies that the larger jaw muscles, rather than merely increasing bite forces, could be involved in other processes that facilitate the consumption of harder, larger prey. Larger jaw muscles might, for example, also help in preventing dislodgment of the lower jaw (De Schepper, 2007) or in maintaining stability during rotational feeding, rather than just increasing bite force.

This potential of broad-heads to consume other prey items than narrow-heads may be crucial when intraspecific competition for prey is high, as it can substantially decrease competition for food and simultaneously increase their survival (Schoener, 1974).

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