

Bimodality in head shape in European eel

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Introduction

The European eel *Anguilla anguilla*, being one of nature's most mysterious animals, has a life cycle that has fascinated scientists ever since it was first commented upon by Aristotle around 350 BC, in his natural history. However, many aspects of its biology, life cycle, migration routes and ecology still remain a mystery (Tesch, 2003; Dekker, 2004; Van Ginneken & Maes, 2006). European eels are not only of scientific interest but also have a long culinary history, being part of the human diet for thousands of years (Ringuelet, Muto & Raymakers, 2002; Schweid, 2004). Consequently, eels have always been an important (economically, aquaculturally and recreationally) fish for fishermen. Today, it is considered of great economical significance, with the 2008 global eel harvest from aquaculture amounting up to 0.26 million tonnes (*A. anguilla* and *Anguilla japonica* combined) (FAO, 2010) and c. 25 000 people across Europe gaining an income from eel fisheries (van Ginneken & Maes, 2006).

Global environmental changes, whether direct or indirect, might be responsible for a lower fat content, which eels store as lipids in their inner organs. Significant decreases in fat levels observed since the late 1970s until 2000 may reflect decreases in food abundance (Wood, 1958; Adjers, Sandström & Bignert, 2000). Lipid content can be influenced by the energy content of the food provided in cultured eels (Garcia-Gallego & Akharbach, 1998), although a decrease in lipid content in

Abstract

The existence of two morphotypes, broadheaded and narrowheaded, in European eels *Anguilla anguilla* is common knowledge among fishermen and eel biologists in Europe. To test whether European eels really are dimorphic in head shape, a total of 277 specimens from two locations in Belgium (Scheldt–Lippenbroek and Lake Weerde), in combination with a larger data set of 725 eels from river systems across Flanders (the northern part of Belgium) were examined. Our biometric data support the hypothesis that a head shape variation in 'Belgian' European eel is best described as having a bimodal distribution. Literature data suggest that this may be the result of phenotypic plasticity related to trophic segregation between morphs.

male silver eels kept for two years under starvation conditions was not observed (Böetius & Böetius, 1985). Although scientific evidence is still fragmentary, low recruitment densities since the last 25 years could have resulted in reduced intraspecific competition, which together with an overall gradual increase in water quality would involve better feeding conditions for the eel.

Despite the existence of two morphotypes in European eels being common knowledge among fishermen, little is known about its ecological significance, or even on the morphological variation. Bimodal variation in head size and shape has been described for populations from Germany (Törlitz, 1922; Thurow, 1958), the Netherlands (Lammens & Visser, 1989) and Ireland (Proman & Reynolds, 2000). These studies show that this variation is linked to ecological variation, where broadheaded specimens tend to be piscivorous and narrowheaded ones feed predominantly on benthic invertebrates (Törlitz, 1922; Thurow, 1958; Lammens & Visser, 1989; Proman & Reynolds, 2000; Tesch, 2003). Interestingly, cultured eels have been shown to be exclusively narrowheaded (Proman & Reynolds, 2000), suggesting that head shape variation may result from environmentally induced phenotypic plasticity (i.e. availability of trophic resources; Lammens & Visser, 1989). Although these observations suggest a plastic response especially to changes in diet, it currently remains unknown whether the morphological variation has a genetic basis as well, or not. Moreover, it is currently unclear whether this

dimorphism is the result of disruptive selection (suggesting an underlying bimodal distribution), or merely reflects the two extremes of a normal distribution.

This study tries to resolve this by providing the first quantitative analysis of head size and shape in the yellow eel stage of *A. anguilla* occurring in Belgium, by testing for a bimodality in head size and shape in populations across a broad range of Flemish water systems.

Material and methods

Study area and sampling procedures

Specimens were captured by fyke nets from the Lippenbroek, a controlled inundation area with reduced tidal movements, and from the river Scheldt (Fig. 1). Yellow eels were collected during April, May, August and October 2006 (monthly samples *c.* 30 specimens). The specimens ($n = 121$ in total) were killed by an overdose of MS222, decapitated, fixed in 10% formalin and preserved in 70% ethanol. Stomachs were removed and the content was analysed for a preliminary diet analysis. Sampling was part of the 'Harmonised River Basin Strategies for the North Sea' (HARBASINS) project (2005–2008) and partially for the MODELKEY project (sub-project 5 – fish communities).

In Lake Weerde (a shallow man-made lake in the Scheldt catchment; Fig. 1), yellow eels were captured by electric fishing and by fyke nets. This lake lacks any open connection with a river system and houses eels from the Flemish glass eel restocking efforts. For this study, eel samples of about 40 specimens each were collected during April, June, July and October 2007. The specimens ($n = 156$) were collected alive and tagged with EID Aalten Trovan pit tags. Pictures of the head (dorsal, lateral and ventral view) were taken. All eels were returned unharmed into Lake Weerde after manipulation. This sampling was part of the INBO – eel pollutant monitoring network and part of an ongoing growth and migration study.

A biometric study of the heads of 725 yellow eels obtained from the INBO-eel pollutant monitoring network (Belpaire & Goemans, 2007) was also performed. Specimens originated from 87 sample sites across Flemish waters between 2001 and 2005 (Fig. 1), and were sampled by electrofishing and fyke netting. Specimens were decapitated and then frozen.

Biometry

In all three batches, total length (TL) was measured with a ruler to the nearest 0.1 cm and body mass was measured to the nearest 0.1 g on fresh specimens.

Scheldt–Lippenbroek sample: 19 head measurements were taken using digital callipers (Mausser) to the nearest

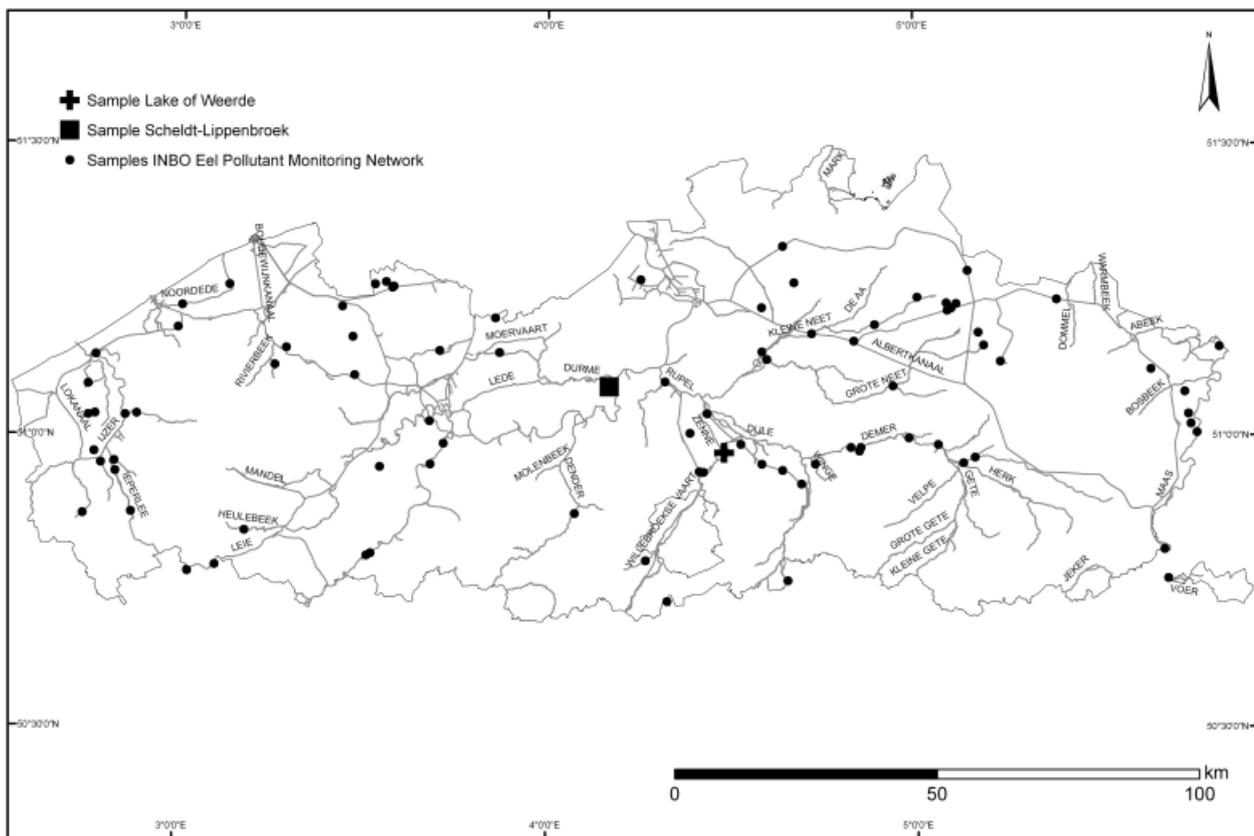


Figure 1 Map of Flanders, Belgium, showing the sampling locations of European eel *Anguilla anguilla* used in this study.

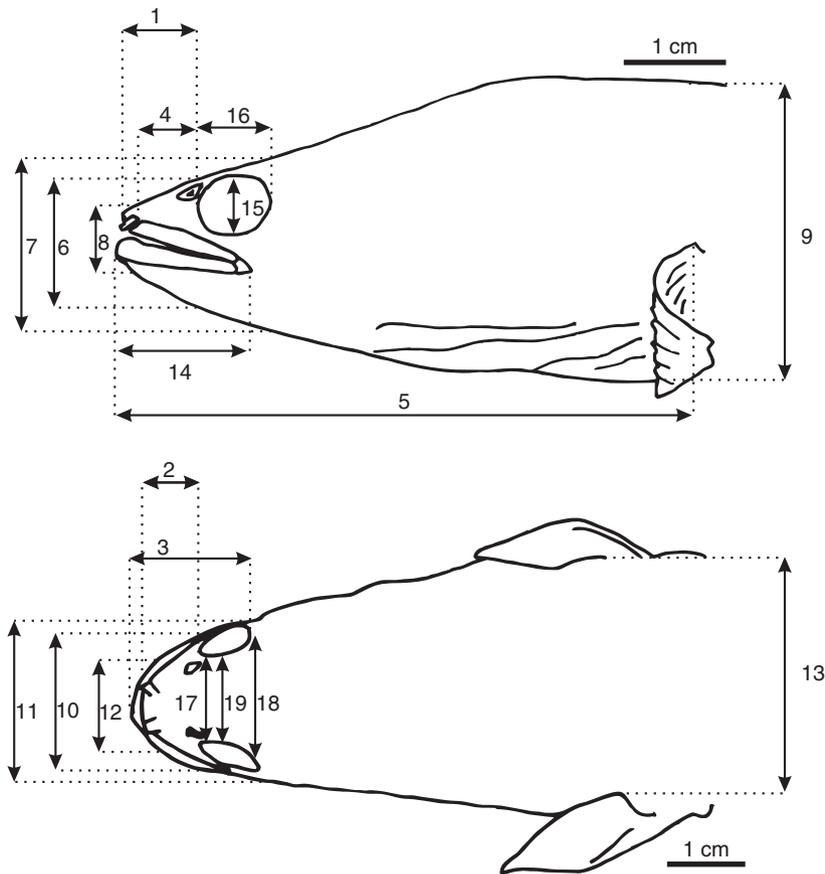


Figure 2 Illustration of the 19 cranial measurements taken on the head of *Anguilla anguilla* (for details, see text).

0.01 mm (Fig. 2): (1) length from the tip of the snout to the rostral border of the eye in lateral view (L Sn-E L); (2) length from the tip of the snout to the rostral border of the eye in dorsal view (L Sn-E D); (3) length from the snout to the caudal border of the eye (L Sn-E c); (4) length from rostral nostril to the rostral border of the eye (L E-nos r); (5) length from the tip of the snout to the pectoral girdle (L Sn-Pe); (6) height of the head at the level of the rostral border of the eye (H H [E r]); (7) height of the head at the level of the caudal border of the eye (H H [E c]); (8) height of the head at the level of the rostral nostril (H H [nos r]); (9) height of the body at the level of the pectoral girdle (H Pe); (10) width of the head at the level of the rostral border of the eye (W H [E r]); (11) width of the head at the level of the caudal border of the eye (W H [E c]); (12) width of the head at the level of the rostral nostril (W H [nos r]); (13) width of the body at the level of the pectoral girdle (W Pe); (14) length of the lower jaw, from the tip of the lower jaw to the angle of the mouth (D); (15) height of the eye (H E); (16) length of the eye (L E); (17) interorbital distance at the level of the rostral border of the eye (IOD r); (18) interorbital distance at the level of the caudal border of the eye (IOD c); (19) interorbital distance at the centre of the eye (IOD m). Specimens were also used for shape analysis.

INBO sample: in 725 specimens, the length from the tip of the snout to the pectoral girdle (L Sn-Pe); interorbital distance

at the centre of the eye (IOD m); height of the head at the level of the caudal border of the eye (H H [E c]); and width of the body at the level of the pectoral girdle (W Pe) were determined.

Lake Weerde sample: used for shape analyses.

Shape analyses

For the specimens from Scheldt–Lippenbroek (only batches from April, May and October) and from Lake Weerde, the outline of the head was drawn based on dorsal view pictures using CorelDraw12. These outlines were then analysed using SHAPE (Iwata & Ukai, 2002). Contours were recorded as chaincodes (a series of numbers between zero and seven that describes the outline) (Kuhl & Giardina, 1982). On the basis of this chaincode, the normalized elliptic Fourier descriptors (EFD's) were calculated (normalized to be invariant with respect to size, rotation and starting point). The size and orientation of the contour are standardized in accordance with the size and alignment of the major axis of the first harmonic ellipse (the latter corresponding to the first Fourier approximation of the contour). A PCA was performed on the normalized EFD's where only the effective components were maintained in the analysis (those components that together explain 95% of the variation), of which the explained the shape variation can then be visualized by the Principal Components Contours.

Analyses

Before the statistical analyses, biometric data were \log_{10} -transformed to assure normality and homoscedasticity. The four subsamples from the Scheldt–Lippenbroek taken at different months proved not to be differed from one another (MANOVA on all measurements: $F_{63,290} = 1.0006$; $P > 0.482$), so samples could be combined for further analyses. To obtain size-independent variation in length measurements, residuals were calculated based on regression analyses for all cranial measurements on TL ($P < 0.05$ for all variables). A normality test (Shapiro–Wilk) was performed on the TL of every sample to test to what degree bimodality in other measurements could be the consequence of TL bimodality.

Four complementary methods were used to infer bimodality (Hendry *et al.*, 2006). (1) Frequency histograms of each \log_{10} -transformed head and TL measurement were examined. (2) For each measurement, the observed cumulative values were plotted against cumulative values expected under normality (plot for single normal distribution is represented by a straight line, whereas bimodal distributions are curved) (Brewer, 2003; Hendry *et al.*, 2006). (3) It was statistically tested (Brewer, 2003; Hendry *et al.*, 2006) whether data from each sample could be best fitted to a single normal distribution or to a mixture of two normal distributions. The fit of a single normal distribution was compared with that of a mixture of two normal distributions with the Akaike's Information Criterion (AIC). The Δ AIC was calculated as AIC for the single normal distribution minus AIC for the fitted mixture of two normal distributions. For interpretation, the following guidelines were used (Brewer, 2003; Hendry *et al.*, 2006): Δ AIC < -8 strongly supports a single normal distribution; $-8 \leq \Delta$ AIC < -5 moderately supports a single normal distribution; $-5 \leq \Delta$ AIC < 5 supports both a single and a mixture of two normal distributions; $5 < \Delta$ AIC ≤ 8 moderately supports a mixture of two normal distributions and Δ AIC > 8 then strongly supports a mixture of two normal distributions. The software routine used for this is developed by Mark Brewer (Software for analysis of mixture models using discretization) and is available upon request (M.Brewer@bioss.ac.uk). This method can only be used to find unimodality or bimodality in a sample. Different samples should not be compared with each other as a correction for sample size is not possible (Δ AIC from one sample can thus be larger just because of a larger sample size) (M. Brewer, pers. comm.). (4) Bimodality was also inferred using the Mixture Analysis using PAST. This is a maximum-likelihood method for estimating parameters (mean, standard deviation and proportion) of two or more univariate normal distributions, based on a pooled univariate sample (Hammer, Harper & Ryan, 2001).

On the pooled samples of Lippenbroek and Weerde, a non-parametric MANOVA was performed in PAST on the PC-scores obtained in the shape-analysis.

Results

Ranges of TL varied but largely overlapped among samples: INBO-sample from 22.9 to 102.3 cm (mean, 42.9 cm),

Scheldt–Lippenbroek sample from 25.6 to 76.0 cm (mean, 45.3 cm) and Lake Weerde sample from 19.2 to 70.3 cm (mean, 40.1 cm). Normality test supported a normal distribution in TL for Lake Weerde ($P = 0.09$), but not for Scheldt–Lippenbroek ($P = 0.01$) and INBO-samples ($P < 0.02$). However, bimodality was also not supported through the Mixture Analysis.

Although sex could not be determined yet in the yellow eels, the distribution of the head shape of eels larger than 50 cm (females are larger than males) was random, and thus sex probably was not related to the dimorphism. Eye index was calculated to distinguish silvering eels in the Scheldt–Lippenbroek sample (could not be performed on the available data for the Lake Weerde and INBO-samples). In the Scheldt–Lippenbroek sample, a total of 25 silvering eels were found, but these were spread over the different head shapes (see Fig. 6a). Hence, silvering could not explain dimorphism. The preliminary diet analysis also confirms the results from Provan & Reynolds (2000), with the broadheaded specimens eating bigger and harder prey items.

Biometry – sample from the Scheldt–Lippenbroek

Variation in cranial measurements shows discontinuities for most of the measurements, suggesting bimodality (Fig. 3a–e). This was not the case for eye length, interorbital distance at the level of the rostral border of the eye and interorbital distance at the caudal border of the eye. However, this does not exclude a bimodal distribution as the overlap between the tails of two distributions can largely fill the gap between them. The plotted cumulative values reveal strong deviation from normality and confirmed a bimodal pattern in the biometric data (Fig. 4). The mixture model approach (Brewer, 2003) also gave a strong support for bimodality in all cranial measurements (Δ AIC > 8) (Table 1). The Mixture Analysis, on the other hand, supports bimodality in all the measurements, except for three: height of the head at the level of the caudal border of the eye, the height of the head at the level of the rostral nostril and the length of the lower jaw. For these measurements, a trimodal distribution fits the data best, a pattern that could not be explained (Fig. 3f).

Broadheadedness and narrowheadedness were shown to be independent of TL. In addition, when an arbitrarily threshold *sensu* Provan & Reynolds (2000) (broadheaded HW/TL > 0.034) was applied and measurements (e.g. IOD c) are plotted versus TL, it becomes clear that broadheadedness is not restricted to the largest specimens (Fig. 5).

Biometry – sample collected from water systems across Belgium (INBO)

The frequency histograms, probability plots and bimodality test of the logarithmically transformed cranial length data in this dataset support a bimodal pattern even more strongly (Table 1). All variables show Δ AIC scores of 203 or higher.

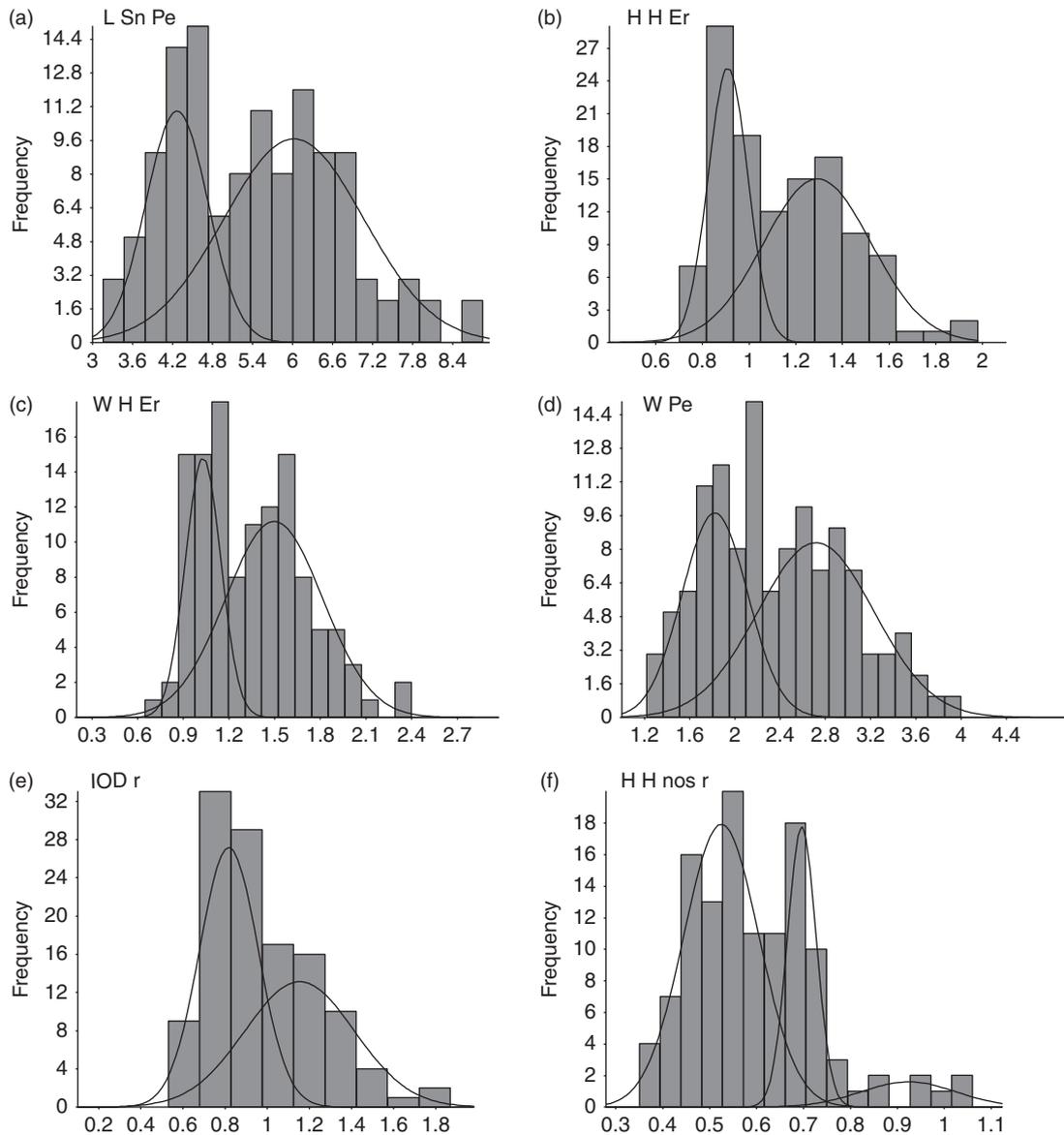


Figure 3 Different distribution patterns of the cranial measurements from European eels *Anguilla anguilla* of the Scheldt–Lippenbroek sample: clear bimodality (a–d); clear bimodal distribution but with strongly overlapping tails (e); and trimodal distribution (f).

Shape analyses

The reconstruction of the Principal Components Contours for the Scheldt–Lippenbroek specimens (Fig. 6a) clearly shows that PC1 (61.2% of the total variation) reflects the variation in the degree of broadheadedness versus narrowheadedness. PC2 (15.1% of the total variation) most probably reflects artificial deformations (asymmetric head bending) as a result of preservation methods and is thus ignored in further analyses. To determine the ratio of narrowheads versus broadheads, we used the number of eels with negative PC1 scores versus the number of eels with positive PC1 scores. When plotting PC1 versus PC3 (7.8% of the total variation), this ratio seems to reflect a temporal pattern with more broadheads sampled in October (Fig. 6a).

In addition, the most extreme narrowheaded ones all come from the April sample and the broadest specimens were caught in October.

The shape analysis of the Lake Weerde sample confirms the largest variation (explained by PC1 – 62.7% of the total variation) reflects the range from broadheadedness to narrowheadedness. As living specimens were used here, none of the PC's reflected the shape variation explained by PC2 in the Scheldt–Lippenbroek sample, hence supporting our assumption that it reflects artefacts due to preservation in the latter. The PC2 (12.8% of the total variation) for the Lake Weerde sample then reflects variation in bluntness of the snout (Fig. 6b). Here, no temporal pattern could be observed in the ratio broadheads – narrowheads over the different periods sampled (Fig. 6b).

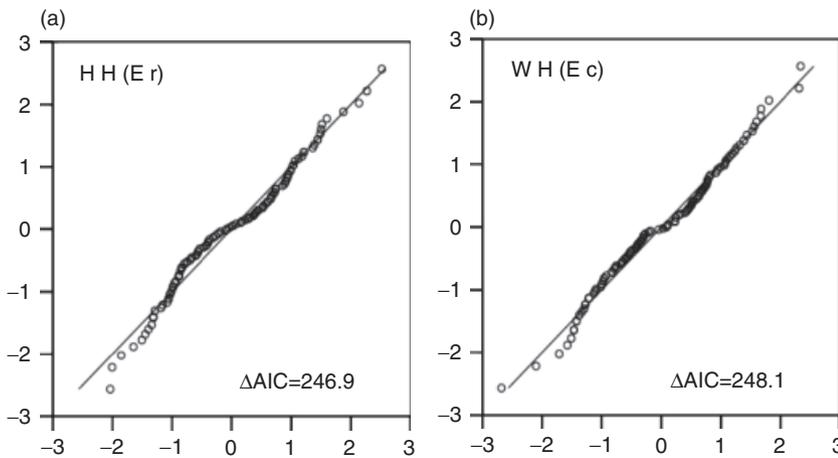


Figure 4 Normality plots of European eels *Anguilla anguilla* of the Scheldt–Lippenbroek sample of (a) head height at the level of the rostral border of the eye (H H [E r]) and (b) width of the head at the level of the caudal border of the eye (W H [E c]).

Table 1 Δ AIC values for all measurements on *Anguilla anguilla* collected in Scheldt–Lippenbroek and water systems across Belgium (INBO) (see text for an explanation of these values)

	Δ AIC
Scheldt–Estuary	
L Sn–E L	228.0
L Sn–E D	243.2
D	239.3
H H (E r)	242.6
H H (E c)	250.2
H E	218.4
L E	233.2
H H (nos r)	210.1
L E–nos r	234.3
W H (E r)	238.8
W H (E c)	247.9
IOD r	243.3
IOD c	243.9
IOD m	231.8
L Sn–E c	273.8
W pe	243.2
H Pe	248.1
L Sn–Pe	260.3
W head nos A	203.9
INBO	
H H (E c)	724.7
IOD m	557.4
L Sn–Pe	1056
W Pe	859.8

In order to see whether there is a difference in head shape between a landlocked population (Lake Weerde) and an estuary population (Scheldt–Lippenbroek), a PCA was also performed on the pooled samples (Fig. 6c). This did reveal that the estuarine sample of Scheldt–Lippenbroek had more extreme broadheads than the landlocked sample from Lake Weerde. A non-parametric MANOVA on the PCA scores ($F = 9.032$; $P < 0.0001$) shows that there is a significant difference in shape between the two groups.

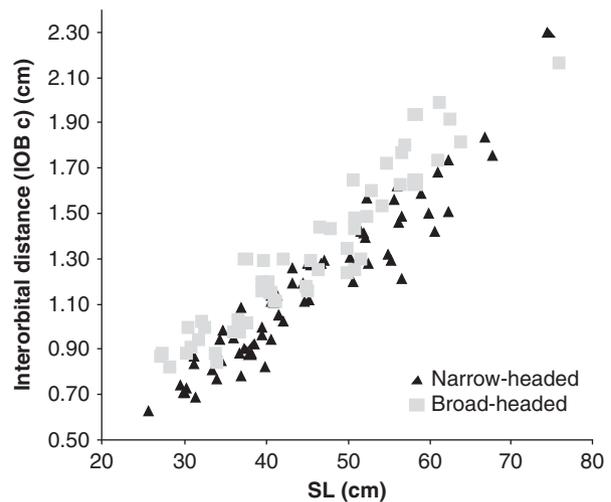


Figure 5 Graph representing size-independence of broadheadedness versus narrowheadedness (interorbital distance at the level caudal border of the eye plotted against total length).

Discussion

Although not yet supported quantitatively, the existence of two trophic morphs in the European eel is widely accepted among fishermen and eel biologists, and is generally considered the result of diet-induced phenotypic plasticity (Lammens & Visser, 1989). The influence of diet on head morphology has been examined in several species, providing support for the hypothesis that different head phenotypes are likely an adaptive response to available trophic resources (Törlitz, 1922; Thurow, 1958; Lammens & Visser, 1989; Stearns, 1989; Provan & Reynolds, 2000; Tesch, 2003; Aubret, Shine & Bonnet, 2004). For example, the trophic ecology of different sparid species is related to their shape, with omnivorous species having a relatively larger head, a larger mouth gape, as well as a different body shape (Costa & Cataudella, 2007). In Dalmatian wall lizards, the different colour morphs, differences in head morphology have been linked to differences in bite performance, with orange males

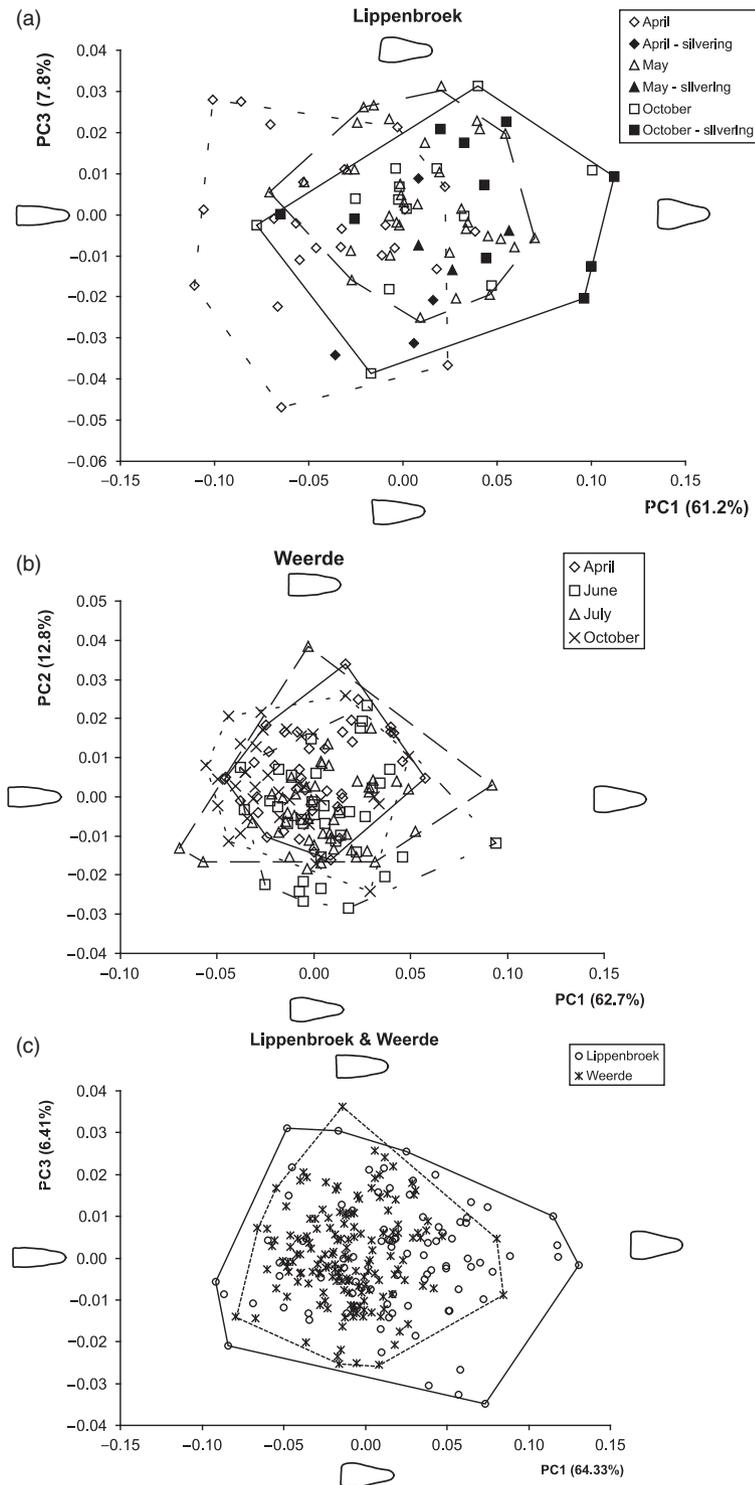


Figure 6 Variation in head shape in *Anguilla anguilla*: (a) PCA plot showing variation in broadheadedness to narrowheadedness in relation to sampling period for the Scheldt–Lippenbroek sample; (b) PCA plot for the Weerde sample; (c) PCA plot of pooled Weerde and Scheldt–Lippenbroek samples, showing that both samples have intermediate forms are similar, but with more extremes in the Scheldt–Lippenbroek sample.

having larger jaw adductors (Huyghe *et al.*, 2009). It has been shown that broadheaded eels also have larger jaw adductors that could be linked to bigger bite forces as well (De Schepper *et al.*, 2007).

In most studied eel populations so far, measurements of mouth widths did not show a clear bimodal distribution (Lam-

mens & Visser, 1989). Moreover, Provan & Reynolds (2000) found that the HW:TL ratio was the only significant correlation with the broadheadedness (eels with HW:TL > 0.033 were considered broadheaded). Our biometric and shape analysis show that morphometric approaches reveal much more substantial support for head shape dimorphism in these Belgian eel

populations. The fact that a clear bimodal distribution could not be detected in previous studies (Lammens & Visser, 1989) may be the result of a strong overlap of the two phenotypes or a lack of rigorous methods testing for bimodality. The results from our study show that bimodality could not always be easily deduced from histograms (Fig. 3e), but needs statistical testing (Brewer, 2003).

Our results reveal that the two phenotypes do, however, not reflect two discrete morphotypes but rather are best described by two normal distributions with overlapping tails. Thus, the shape of the heads of specimens can also be intermediate (Fig. 6a and b), which complicates discrete characterization of the two phenotypes. The most important differences between phenotypes in our biometric study are observed at the level of the jaw length, head width and head height, as was suggested previously by Törlitz (1922) and Thurow (1958).

Ecologically relevant is the fact that both broad- and narrowheaded eels occur syntopically in the Scheldt–Lippenbroek, in Lake Weerde and in general in waters across Flanders. Selective pressure associated with population density and prey diversity or abundances could be the driving forces maintaining the syntopy of the morphotypes. Indeed, high-population densities in eels could drive segregation in trophic ecology and hence in phenotype (see also Lammens & Visser, 1989). For the sample of the Scheldt–Lippenbroek, the higher proportion of broadheads relative to narrowheads over the sampling periods could be the result of a temporal shift in the abundance of prey items, especially fish. Migration of fish species from the river Scheldt into the Lippenbroek has been demonstrated by Simoens *et al.* (2007). As it seems unlikely that such a seasonal shift in the availability of prey fishes would then lead to a rapid shift in the head phenotype, a migration of eels in accordance with prey would be more likely.

If phenotypic plasticity explains the observed variation, with both phenotypes having different prey preferences (Proman & Reynolds, 2000; Lammens & Visser, 1989), shifts in the ratio of both phenotypes in natural populations may also have an impact on freshwater ecosystems. As such, the observation that eels raised in captivity are exclusively narrowheaded (Proman & Reynolds, 2000) indicates the need for well-planned management actions when restocking farm-raised specimens. This, however, also suggests the inverse relationship, where a phenotypic response is triggered by the environment. Changes in the trophic ecosystem, whether natural or anthropogenic, may then also induce shifts in the ratio of both phenotypes. This potentially two-way relationship between phenotype and ecology suggests that efforts towards conservation may require the assessment of morphological variation within the population and its proximate causes.

Interestingly, the biometric sample of eels dispersed across Flemish waters also reveals bimodality, thus suggesting that the occurrence of the two phenotypes is not a local phenomenon. The existence of a dimorphism for eels in Germany (Törlitz, 1922; Tesch, 2003), the Netherlands (Lammens & Visser, 1989) and Ireland (Proman & Reynolds, 2000) even suggests that it is widespread throughout Europe and may be present in the whole panmictic population (Dannewitz *et al.*, 2005).

Bimodality in head shape has also been suggested for Japanese eels (Thurow, 1958). Interestingly, such a head dimorphism has not been suggested for the American eel, despite the morphological resemblance, close phylogenetic relationship, similar life cycle and spawning grounds to the European eel (Tesch, 2003; Trautner, 2006). It would thus be worth testing for bimodality in American eel head shape.

In other fishes such as sticklebacks, different habitats (lakes vs. streaming water) have been related to both morphological and dietary differences (Berner *et al.*, 2008), as well as the presence–absence of natural predators (Walker, 1997). For European eels, the situation is in this way different that variation in phenotype and ecology is observed within the same habitat, such that the presence or absence of predators also could not be the explanatory factor leading to this dimorphism. Trophic segregation within the same habitat at this point still provides the best explanation, but feeding experiments would be required to actually test this hypothesis properly. It is important to note, however, that even though data from literature appear to support the hypothesis that head-shape variation in European eels is a phenotypically plastic response, the possibility of genetic variation inducing the dimorphism cannot be excluded and should be examined in future studies.

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References

- Ådjers, K., Sandstöm, O. & Bignert, A. (2000). Fisk och fiske – fisketrycket för hårt (fishery in trouble with English summary). In *Östersjö '99 Årsrapport från miljöövervakningen I egentliga Östersjön (Swedish marine monitoring in the Baltic Proper)*: 35–36. Tidlund, A. & Brenner, U. (Eds). Stockholm: Stockholm Marine Research Center.
- Aubret, F., Shine, R. & Bonnet, X. (2004). Adaptive plasticity in snakes. *Nature* **431**, 261–262.
- Belpaire, C. & Goemans, G. (2007). The European eel, *Anguilla anguilla*, a rapporteur of the chemical status for the Water Framework Directive? 12 years of monitoring in Flanders. *Vie et Milieu – Life Environ.* **57**, 235–252.
- Berner, D., Adams, D.C., Grandchamp, A.-C. & Hendry, A.P. (2008). Natural selection drives patterns of lake-stream divergence in stickleback foraging morphology. *J. Evol. Biol.* **21**, 1653–1665.
- Böetius, I. & Böetius, J. (1985). Lipid and protein content in *Anguilla anguilla* during growth and starvation. *Dana* **4**, 1–17.

- Brewer, M.J. (2003). Discretisation for inference on normal mixture models. *Stat. Comput.* **13**, 209–219.
- Costa, C. & Cataudella, S. (2007). Relationship between shape and trophic ecology of selected species of Sparids of the Caprolace coastal lagoon (Central Tyrrhenian sea). *Environ. Biol. Fish* **78**, 115–123.
- Dannewitz, J., Maes, G., Johansson, L., Wickström, H., Volckaert, F. & Järvi, T. (2005). Panmixia in the European eel: a matter of time *Proc. R. Soc. Lond. Ser. B* **272**, 1129–1137.
- Dekker, W. (2004). What caused the decline of the Lake IJsselmeer eel stock after 1960? *ICES J. Mar. Sci.* **61**, 394–404.
- De Schepper, N., Van Liefveringe, C., Herrel, A., Goemans, G., Belpaire, C. & Adriaens, D. (2007). *Cranial musculature of Anguilla anguilla (Anguilliformes): Functional implications related to narrowheadedness and broadheadedness*. In: *Evolutionary morphology of body elongation in teleosts: aspects of convergent evolution*. PhD dissertation, Ghent University, Ghent, Belgium, 292pp.
- FAO (2010). *The state of World Fisheries and Aquaculture 2010*. Rome: : FAO, 197pp.
- ICES (2006). *Report of the 2006 session of the Joint EIFAC/ICES Working Group on Eels. FAO European Inland Fisheries Advisory Commission: International Council for the exploration of the Sea, Rome 23–27 January 2006*. EIFAC Occasional Paper. No. 38, ICES CM 2006/ACFM: 16. FAO/Copenhagen, ICES, Rome, 352pp.
- Garcia-Gallego, M. & Akharbach, H. (1998). Evolution of body composition of European eels during their growth phase in a fish farm, with special emphasis on the lipid component. *Aquac. Int.* **6**, 345–356.
- Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaentol. Electron.* **4**, 1–9.
- Hendry, A.P., Grant, P.R., Grant, B.R., Ford, H.A., Brewer, M.J. & Podos, J. (2006). Possible human impacts on adaptive radiation: beak size bimodality in Darwin's finches. *Proc. Roy. Soc. Lond. Ser. B: Biol. Sci.* **273**, 1887–1894.
- Huyghe, K., Herrel, A., Dominique, A., Tadić, Z. & Van Damme, R. (2009). It is all in the head: morphological basis for differences in bite force among colour morphs of the Dalmatian wall lizard. *Biol. J. Linn. Soc.* **96**, 13–22.
- Iwata, H. & Ukai, Y. (2002). A computer program package for quantitative evaluation of biological shapes based on elliptic Fourier descriptors. *J. Hered.* **93**, 384–385.
- Kuhl, F.P. & Giardina, C.R. (1982). Elliptic fourier features of a closed contour. *Comput. Graph. Image Process.* **18**, 236–258.
- Lammens, E.H. & Visser, J.T. (1989). Variability of mouth width in European eel, *Anguilla anguilla*, in relation to varying feeding conditions in three Dutch lakes. *Environ. Biol. Fish.* **26**, 63–75.
- Proman, J.M. & Reynolds, J.D. (2000). Differences in head shape of the European eel, *Anguilla anguilla*. *Fish. Mgmt. Ecol.* **7**, 349–354.
- Ringuet, S., Muto, F. & Raymakers, C. (2002). Eels: their harvest and trade in Europe and Asia. *Traffic Bull.* **19**, 2–27.
- Schweid, R. (2004). *Consider the eel, a natural and gastronomic history*. Chapel Hill: Da Capo Press, University of North Carolina Press.
- Simoens, I., Breine, J., VanLiefveringe, C., Stevens, M. & Belpaire, C. (2007). Het belang van het Lippenbroek als habitat voor vissen in de Zeeschelde. In: *Congres Watersysteemkennis 2006/2007: Mogelijkheden voor ecologisch herstel van watersystemen*. *Water: Tijdschrift over Integraal Waterbeleid*, 30: pp. 68–71.
- Stearns, S.C. (1989). The evolutionary significance of phenotypic plasticity. *Bioscience* **39**, 436–445.
- Tesch, F.W. (2003). *The eel*, 5th edn. Oxford: Blackwell Science.
- Thurow, F. (1958). Untersuchungen über die spitz und breitköpfigen Varianten des Flusssaales. *Arch. Fisch. Wiss.* **9**, 79–97.
- Törlitz, H. (1922). Anatomische und entwicklungsgeschichtliche Beiträge zur Artfrage unseres Flusssaales. *Z. Fisch.* **21**, 1–48.
- Trautner, J. (2006). Rapid identification of European (*Anguilla anguilla*) and North American eel (*Anguilla rostrata*) by polymerase chain reaction. *Inf. Fisch.* **53**, 49–51.
- Van Ginneken, V. & Maes, G. (2006). The European eel (*Anguilla anguilla*, Linnaeus), its lifecycle, evolution and reproduction: a literature review. *Rev. Fish. Biol. Fish.* **15**, 367–398.
- Walker, J.A. (1997). Ecological morphology of lacustrine threespine stickleback *Gasterosteus aculeatus* L. (Gasterosteidae) body shape. *Biol. J. Linn. Soc.* **61**, 3–50.
- Wood, R.J. (1958). Fat cycles of North Sea herring. *ICES J. Mar. Sci.* **23**, 390–398.