Integrative and Comparative Biology

*Integrative and Comparative Biology*, volume 60, number 2, pp. 467–475
doi:10.1093/icb/icaa004

*Society for Integrative and Comparative Biology*

SYMPOSIUM

# Saving the European Eel: How Morphological Research Can Help in Effective Conservation Management

Jens De Meyer ,* Pieterjan Verhelst,† and Dominique Adriaens*

*Evolutionary Morphology of Vertebrates, Ghent University, K.L. Ledeganckstraat 35, Ghent 9000, Belgium; †Marine Biology, Ghent University, Krijgslaan 281, Ghent, 9000, Belgium

From the symposium "Applied Functional Biology: Linking Ecological Morphology to Conservation and Management" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2010 at Austin, Texas.

[1]E-mail: Jendmeye.demeyer@ugent.be



**Synopsis** The European eel (*Anguilla anguilla*) is a critically endangered species, whose recruitment stocks have declined to nearly 1% compared to the late 70s. An amalgam of factors is responsible for this, among them migration barriers, pollution, habitat loss, parasite infection, and overfishing. A lot of recent studies focus on aspects that can increase the mature silver eel escapement rate, such as identifying migration barriers and developing passageways or addressing the impact of pollution on the eel's health. However, little attention is given to the eel's morphology in function of management measures. Worryingly, less than 50% of the currently installed management plans reach their goals, strongly indicating that more information is needed about the eel's ecology and behavior. Functional morphological studies provide insights on how species perform behaviors crucial for survival, such as feeding and locomotion, but also in how environmental changes can affect or limit such behaviors. Consequently, functional morphology represents an important biotic component that should be taken into account when making conservation decisions. Hence, here, we provide an overview of studies on the eel's morphology that do not only demonstrate its relation with ecology and behavior, but also provide information for developing and installing proper and more specific management measures.

## Introduction

The panmictic population of the facultative catadromous European eel (*Anguilla Anguilla*; Fig. 1) has been declining extensively, with the current glass eel recruitment having decreased to nearly 1–5% compared to the late 1970s (Bark et al. 2007; Freyhof and Brooks 2011). Consequently, the European eel is considered a critically endangered species according to the IUCN Red List (Jacoby and Gollock 2014). An amalgam of factors are responsible for this decline: Shifts in the Gulf Stream that reduce leptocephalus larvae survival during transoceanic migration, overfishing, and poaching, the presence of upstream and downstream migration barriers, habitat loss and deterioration, infection by invasive, non-native parasites, and pollution (Drouineau et al. 2018). In addition, eel stocks in suitable habitats are declining because the departure of the emigrating silver eels is not compensated by the arrival of new, young eels (Nzau Matondo et al. 2019). In order to preserve and potentially restore the European eel population, the European Council has put the EU Eel Regulation in place (EC 1100/2007). This regulation requires that all the EU member states where the European eel is native establish eel management plans at a river basin scale. The goal of these plans is to obtain a silver eel biomass escapement to the sea of at least 40%, compared to the estimated stock levels in the absence of human influences. This percentage could be reached by reducing fisheries, improving habitats, overcoming migration barriers, restocking eels to suitable habitats with limited to no natural migration, and transporting silver eels directly to the sea. The regulation also states that, from 2013, 60% of the annually caught eels smaller than 12 cm should be used for restocking only. Despite these measures, the European eel population still continues to decrease. Even more, 42 out

Advance Access publication February 28, 2020

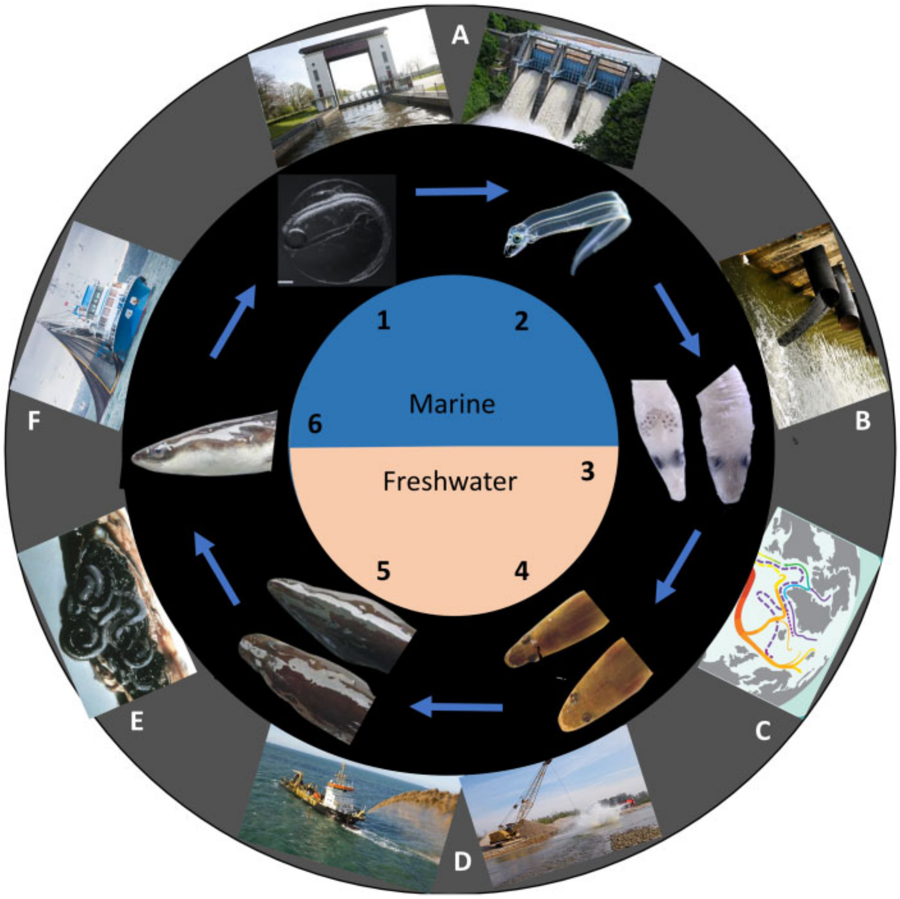


**Fig. 1** Life cycle (inner circle) and threats (outer circle) of the European eel. The European eel spawns in the Sargasso Sea. From the eggs (1) hatch leptocephalus larvae (2), which are transported toward the coasts of Europe, along with the Gulf Stream. Arriving at the European continental shelves, the larvae transform into unpigmented glass eels (3), which swim up the rivers. There, eels start to feed and become pigmented. Fully pigmented eels smaller than 10 cm are considered elver eels (4). Once the eels grow larger, they reach the yellow eel stage, the sedentary growth phase (5). When enough fat is stored, the eels undergo a final metamorphosis to the silver eel stage (6) during their migration toward the Sargasso Sea. Heads on the outside of the circle represent broad-headed phenotypes, heads on the inside narrow-headed phenotypes. The threats of the European eel include migration barriers (A), pollution (B), climate change (C), habitat loss and deterioration (D), infection by *Anguillicoloides crassus* (E) and overfishing (F). © Figures: Curren (A); Nrdc (B); EJatlas (D-right); Ihc (D-left); Hellen Gilbert (F); Google Images (C, E); Atmosphere and Ocean Institute, Tokyo University (1).

of 81 Eel Management Plan reports indicated not to achieve the 40% biomass escapement goal, even though 20 of them are trending toward reaching the goal in the future. Only 17 reports actually reached the 40% biomass escapement, of which 11 are expected to be below the 40% target in the future (ICES 2013). Hence, much more effort is required to restore this species to healthy population levels.

A thorough knowledge of the eel's ecology and behavior is paramount to establish proper management plans. With a higher silver eel biomass escapement rate as one of the major goals, it should not be surprising that many recent studies focus on eel migration (Stein et al. 2016; Okland et al. 2017; Piper et al. 2017; Verhelst et al. 2018a), developing proper passage solutions (Egg et al. 2017; Jellyman et al. 2017; Fjeldstad et al. 2018; Tamario et al. 2019; Watz et al. 2019), and assessing the impact of hydropower stations, parasites, fisheries, and pollution on the eel population (Winter et al. 2006; Belpaire et al. 2016; Foekema et al. 2016; Dainys et al. 2018; Pedersen and Rasmussen 2018; Simon et al. 2018; Heisey et al. 2019). While such studies are pivotal for eel conservation, it also highlights the limited attention for other aspects. One such aspect that remains generally understudied is the eel's morphology. Functional morphology is, however, tightly related to how species perform key behaviors, such as feeding and locomotion, and consequently provides crucial insights into its survival and fitness (Arnold 1983, 2003; Irschick 2003; Schoenfuss and Blob 2007). Moreover, insights into functional morphology can allow to determine the potential effects of environmental alterations on a species' performance. In the most extreme cases, abrupt environmental changes caused by human activities can invoke dramatic population decreases (Holland 1986; Wolter and Arlinghaus 2003). Because of this, functional morphology should be considered an important component in establishing proper management plans. The goal of this article is to provide an overview of how previous and future (functional) morphological research can play a role in the conservation of the European eel.

## Body size and substrate preference

Body size is one of the most important morphological traits affecting the swimming performance of fish. In general, continuous swimming speed tends to increase with body size, whereas maneuverability decreases with body size. Acceleration, on the contrary, important for predator-avoidance responses is size-independent (reviewed in Domenici 2001). Many anguilliform fish are, however, also known to burrow into the substrate (Herrel et al. 2011). Still, whether body size affects burrowing behavior in eels has not been evaluated yet. On the one hand, the plumber, heavier body of larger eels can experience more drag during burrowing (Vogel 1994), whereas on the other hand, large eels could generate higher burrowing forces to dig into harder, denser substrates. Consequently, body size cannot only affect burrowing efficiency but also the exploitable and preferred bottom substrate.

Simultaneously, anthropogenic activities such as dredging, the extraction of sand and gravel (de Groot 1996; Desprez 2000; Gage et al. 2005; ICES 2016), and even ship passage can seriously affect the bottom substrate and thus impact the eel's (potential) habitat. Determining whether there is a size-dependent substrate preference in the European eel is thus crucial to determine the impact of such activities on the eel population, but can also provide important information for habitat restoration and selecting the most suitable habitats for restocking.

As such, Christoffersen et al. (2018), Petterson (2019), and Steendam (2019) evaluated substrate preference in European eel, the former two in a single life stage, the latter in all sedentary life stages. Interestingly, substrate preference tends to change during the eel's ontogeny and depends on the eel's body size. Unpigmented glass eels and the subsequent elver eels show a preference for coarse gravel (Ø < 8 mm; Christoffersen et al. 2018; Petterson 2019; Steendam 2019). However, once the eels reach the fully pigmented yellow eel stage, an increasing preference for fine gravel is observed. Sandy substrates, on the contrary, were the least preferred substrates in all life stages. Steendam (2019) showed that this can be linked to burrowing speed and effort, as burrowing into sandy substrates required more time and more body undulations, and thus more energy, compared to burrowing into fine gravel substrates. The observation that the eel's substrate preference changes with body size has important implications for future eel management plans. In general, a distinction can be made between the youngest sedentary life stages (glass and elver eels) and the older, larger yellow eel stage. Measures in terms of habitat restoration and restocking should, therefore, take into account eel size.

The young glass eels and elvers showed a clear preference for coarse gravel, because the spaces between the grains provide easy shelter (Steendam 2019). Larger yellow eels, which can no longer hide between the interstitial spaces, showed a preference for fine gravel, which allows easy burrowing. Hence, despite the lower urge for these larger eels to burrow (Steendam 2019), shelter remains important to avoid predation. The preservation and/or provision of materials that allow shelter, including fine and coarse gravel, cobbles, but also abundant aquatic vegetation at shores and underwater, could therefore play an important role in supporting eel survival. Moreover, shipping canals and canalized rivers provide little to no shelter for eels due to the lack of "natural features"; they consist of steep walls with limited vegetation or natural materials in the water, such as trees and large branches, as these are removed to allow safe ship passage. Such systems might thus benefit from substrate measures, such as the construction of coarse and fine gravel beds. While the previously mentioned studies have already taken the initial steps in understanding substrate preference and use in the European eel, more thorough studies on these matters can allow the proposition of effective management measures in terms of habitat restoration.

Also in terms of restocking, diversified habitats that provide easy shelter should be prioritized as the more suitable the habitat, the more likely the eels are to survive (Nzau Matondo et al. 2019). Such habitats preferably contain coarse gravel substrates for glass and elver eels and fine gravel substrates for yellow eels, ideally combined with dense vegetation.

Finally, substrate preference might help in developing more efficient ladders that allow eels to cross migration barriers. Eel ladders provide a climbing substrate under the form of mats covered by bristles or synthetic materials, arranged in a pattern that allows eels to pass between them, while using the bristles themselves as push-off points (Legault et al. 1990). Glass and elver eels are typically attracted toward these ladders by some form of attractant water flow. However, the substrate preference of these eels shows that coarse gravel material could be used as a natural alternative for the bristles and synthetic materials currently used in eel ladders, as glass eels can easily move through the interstitial spaces. Alternatively, small coarse gravel zones can be installed around passageways, providing easy shelter for glass and elver eels where they can safely recover from failed climbing attempts. Simultaneously, such zones can play a role in reducing the predation risk at accumulation zones such as migration barriers.

## Head shape: Key role in installing efficient conservation measures?

Variation in head shape has been of interest to functional morphologists for decades, because it plays a role in several key functions, such as prey capture, feeding, burrowing, and agonistic interactions (Cooper and Vitt 1993; Herrel et al. 2001; Lappin and Husak 2005; Losos 2009; Vanhooydonck et al. 2011). Interestingly, Törlitz (1922) reported that head shape is dimorphic in the European eel, distinguishing broad- from narrow-headed eels (Fig. 1). Since then, this phenomenon has been observed in other studies as well (Thurow 1958; Lammens and Visser 1989; Proman and Reynolds 2000; Ide et al. 2011). While a more recent study showed that head shape is not dimorphic in all-natural habitats (Verhelst et al. 2018b), extensive variation in head shape was still observed. The presence of a dimorphic head shape, presented as a bimodal distribution with overlapping tails (Ide et al. 2011), suggests that there is disruptive selection toward extreme phenotypes in European eel.

Such a dimorphism is generally linked to a trade-off between different performance traits. In most cases, broad-headed morphs are associated with higher bite forces as broader heads allow the accommodation of larger jaw muscles. Studies on the underlying musculoskeletal system confirmed that this is also the case in European eel (De Meyer et al. 2018b, 2018c, 2018d). The observed differences in head shape and bite force have been related to dietary differences between narrow- and broad-headed morphs. Stomach content analyses found that broad-headed eels fed proportionally more on harder, larger prey items, such as crustaceans and fish, while narrow-headed eels consumed predominantly soft, small prey, such as chironomid larvae (Lammens and Visser 1989; Tesch 2003). A more recent study by De Meyer et al. (2018a), using stable isotope analysis, showed that with increasing head width the trophic position of the eel increased, independent of age and size, confirming the earlier results of Cucherousset et al. (2011). As such, the broader the head of the eel, the better it is suited for feeding on larger prey items and the proportionally more it will consume these prey items. Hence, there is a clear link between morphology, performance, and diet/trophic position.

Simultaneously, the observation of disruptive selection suggests that having a narrow head should be advantageous over intermediately shaped heads as well. Nevertheless, the advantage of a narrow head has yet to be determined. A narrow head can, for example, decrease hydrodynamic drag during prey-capture bursts, but as narrow-headed eels feed on slower, less elusive prey than broad-headed eels, it seems unlikely that a narrow head is selected for in terms of diet. Interestingly, however, head shape dimorphism has also been established to be a potential trade-off between increasing bite force versus increasing burrowing efficiency (Teodecki et al. 1998; Vanhooydonck et al. 2011). Having a narrow head can be expected to decrease drag/friction during burrowing (Van Wassenbergh et al. 2010; Van Wassenbergh et al. 2015) and thus can facilitate burrowing behavior. From a functional morphological view, it would be interesting to determine whether narrow-headed eels are indeed capable of burrowing more efficiently than broad-headed morphs. If this would be the case, there might be a difference in habitat occupation between differently shaped eels. Accordingly, Cucherousset et al. (2011) already observed that broad-headed eels occupy more open, deeper waters, whereas narrow-headed eels are mainly found near the river banks. These different habitats do not only match with the differences in consumed prey items, but could also correspond to differences in burrowing behavior.

Next to habitat differences, Barry et al. (2016) also found behavioral differences between the eels: Broad-headed eels occupy a homing range twice the size of narrow-headed eels and are nocturnally active, whereas narrow-heads are more crepuscular.

As such, broad- and narrow-headed eels could occupy different niches in terms of diet, habitat, and even behavior. Consequently, these eels might be differently affected by anthropogenic threats and require different conservation measures.

### Head shape, diet, pollution, and parasite infections

Pollution is one of the contributors to the eel's decline that might have a varying effect on differently shaped eels. An important component of a pollutant is its lipophilicity; the more lipophilic a pollutant is, the more likely it is to accumulate in the food chain, a process known as biomagnification. The difference in trophic position between broad- and narrow-headed eels can thus result in a difference in pollutant accumulation as well. To determine whether this is the case, De Meyer et al. (2018a) studied the relation between head shape, trophic position, and pollutant accumulation. They found that broad-headed eels accumulate more lipophilic pollutants than narrow-headed eels, independent of size and age. Additionally, they show that the more lipophilic a pollutant is, the more it will accumulate in broad-headed eels. These results thus indicate that head shape, through its relation with diet, will impact pollutant accumulation. The higher levels of lipophilic pollutants can impact broad-headed eels on four different levels, as proposed by De Meyer et al. (2018a); (1) first, pollutants are known to disturb the fat metabolism, by causing chemical stress which increases the eel's energetic demand. Broad-headed eels might thus require a prolonged fat accumulation period (Robinet and Feunteun 2002; Geeraerts and Belpaire 2010) to store enough energy reserves (at least 12% of body weight) before being able to start migration. Accordingly, De Meyer et al. (2018a) found lower fat percentages in broad-headed eels compared to narrow-headed ones. The prolonged fat accumulation period required by broad-headed eels also makes them more vulnerable to other threats such as predation. (2) Broad-headed eels might start their 6500 km migration toward the Sargasso Sea with insufficient energy stores to successfully reach the Sargasso Sea and produce gametes. (3) As eels stop feeding during migration, the stored fat tissue is being metabolized, releasing the stored lipophilic pollutants inside the body where they can disturb the immune, nervous, reproduction, and endocrine system (Geeraerts and Belpaire 2010). (4) Finally, the higher levels of toxic pollutants in broad-headed eels can interfere with ovary development (Johnson et al. 1998), decreasing the mean weight, and thus viability, of their eggs. The combination of these effects shows that pollution can have detrimental effects on the reproductive success of especially broad-headed eels.

The difference in diet between broad- and narrow-headed eels can, however, not only cause differential pollutant uptake. In the 1980s, the nematode parasite *Anguillicoloides crassus* was introduced from Asia into Europe. Since its introduction, this parasite has been infecting the freshwater life stages of the European eel (Kirk 2003), damaging the swim bladder and thus impairing the eel's swimming performance (Lefebvre et al. 2013). Furthermore, the parasite drains the eel's highly necessary energy during migration by blood suction (Neto et al. 2010). The parasite infection can thus substantially disturb successful spawning migration (Palstra et al. 2007; Barry et al. 2014; Pelster 2015). Because of this, *A. crassus* infections are considered one of the factors driving the European eel decline. In Europe, the parasite uses a wide range of species as host, primarily fish (Szekely 1994; Kennedy 2007). Several studies have shown that the consumption of these fish hosts leads to increased transmission rates to European eels (Szekely 1994; Sures and Streit 2001; Kirk 2003; Knopf and Mahnke 2004). Since broad-headed eels are higher in the food chain and more piscivorous (Cucherousset et al. 2011; De Meyer et al. 2018a), they are more likely to be exposed to this parasite than narrow-headed eels. A recent study by Pegg et al. (2015) indeed confirmed that with increasing head width, the prevalence of *A. crassus* increases as well. Broad-headed eels are thus also more likely to suffer from parasite infections than narrow-headed eels. The synergetic effect of higher pollutant levels and more prevalent *A. crassus* infections might crucially impair the broad-headed eel's migration success.

These results have interesting implications for eel conservation. First, it shows that monitoring the European eel population in its freshwater life stages can result in underestimating its actual health status. Eels in the freshwater stages do not necessarily contribute to future generations, as most detrimental effects of pollution and parasitism will only become apparent once the eel is migrating. Moreover, in highly polluted environments, especially broad-headed eels might be at risk of not contributing at all. Simultaneously, head shape could be used as a proxy for determining the eel's health and trophic status at different capturing sites because of its established link with diet, pollution levels, and parasite infections. Second, the biomagnifying effect indicates that current conservation measures need to put more effort in further improving aquatic habitat. Not only enhancing water but also substrate quality by removing pollutants should be implemented as one of the priorities in eel management plans.

Finally, because the eel stores pollutants in its fat tissue during its freshwater life stages, it has also been proposed as a suitable bioindicator of the chemical status within water framework directives (Belpaire and Goemans 2007). If European eels would be used as bioindicator, it should be taken into account that variation in trophic position, for which head shape can be used as a proxy, can be an important confounding factor in interpreting the results. Sample sizes should thus be large enough to have a range of morphologically different eels at each sample site in order to obtain reliable results.

### The relevance of head shape variation in eel conservation

Pollution and parasitism have an increased impact on broad-headed eels, which can impair both their survivability and spawning success. In addition, work by Simon (2007) showed that overfishing can indirectly affect broad-heads by removing their prey items. This has led to a steep decrease of broad-headed eels compared to narrow-headed eels in Lake Sacrow in Germany. The cumulative effects of pollution, parasitism, and overfishing indicate that narrow-heads could strongly dominate the European eel population in current and future generations. How this selection toward narrow-heads might affect the eel population and whether it will have a negative impact on future generations is not known yet. Broad- and narrow-headed eels occupy a different trophic position and habitat and are active during different periods (Cucherousset et al. 2011; Barry et al. 2015). This exploitation of different niches allows more eels to co-exist at a single location. Due to the dominance of one eel phenotype or a reduction in head shape variation, these positive population effects might be (strongly) reduced or even be lost. In the worst case, a decreased contribution of broad-headed eels to future generations might lead to genetic loss, as De Meyer et al. (2017) found evidence that at least part of the head shape variation in European eels is caused by differential gene expression. Simultaneously, De Meyer et al. (2016) found that eels reared on different diets develop different head shapes as well, and head shape variation might thus also be partially a plastic response to the consumed prey. As such, the current lack of crucial knowledge about the mechanisms behind head shape variation does not allow to determine possible long-term effects of changes in the relative abundance of broad-heads versus narrow-heads. Consequently, from a precautionary perspective, current management measures should assure that head shape variation is maintained.

Moreover, it should be evaluated whether conservation measures have a varying effect on differently shaped eels. In addition, monitoring the relative broad-head/narrow abundance is important to evaluate the effects of these shifts on local and more global scale. Knowing these relative abundances can also optimize the effectiveness of restocking. It can allow not only to determine which habitats are suited for which phenotypes, but also to prevent the release of too many similarly shaped eels which could have profound effects on intra-specific competition.

Functional morphologists can play an important role in these processes by establishing clear criteria to define broad- and narrow-headedness, by identifying the mechanisms behind head shape variation in cooperation with geneticists and ecologists, and by assisting in determining the effects of conservation measures on eels with a different phenotype.

## Hydrodynamics and proper passage

The shape of a fish, as well as the way it moves, influences the water flow past the body (Walters 1962). Eels have a long, narrow body and swim by undulating the body and the caudal fin (Webb 1984), which allows for energy-efficient swimming (Palstra et al. 2008). Even more, van Ginneken et al. (2005) found that eels can swim four to six times more energy-efficient than non-eel like fish, enabling them to successfully migrate toward the Sargasso Sea (van den Thillart et al. 2004). Tytell and Lauder (2004) and Tytell (2004) found that eel swimming can have a relatively high hydrodynamic efficiency of 50 up to 87%, where an efficiency of 100% would mean that all the power of a lateral undulation would be used for forward motion. However, morphological variation could have an impact on this efficiency. Narrow, bullet-shaped heads are, for example, expected to experience less hydrodynamic drag during swimming than broad, blunt heads and could, therefore, have a higher efficiency, which, in turn, might result in a better swimming performance. A study by Verhelst et al. (2018b) found no relation between migration speed and head width among eels, but this does not exclude potential differences in swimming performance. In addition, there is sexual dimorphism in size, with males reaching a maximum body size of 45 cm, whereas females reach lengths up to 133 cm (Dekker et al. 1998). Females will thus have a plumber, heavier body than males, which can impact the experienced drag as well (Vogel 1994). Whether such differences in size and shape have an impact on the experienced drag, the hydrodynamic efficiency, and swimming performance have not been tested yet. Insights into these relationships might prove fruitful in terms of conservation as well, for instance, in optimizing eel passageways. Indeed, a lot of studies have been conducted to improve the effectiveness of eel ladders by means of different materials, different angles at which eels require to move upward (Legault et al. 1990; Legault 1992). Insight in the hydrodynamic implications of the morphology can help in determining appropriate materials, in identifying proper patterns and distances between brushes for eel ladders. Furthermore, if swimming performance and/or experienced drag is related to morphology, the suitability of different passage types might depend on eel morphology as well. It is, for example, possible that large and broad-headed eels will experience more drag due to their less suitable hydrodynamic morphology. Crossing passageways for such eels might thus require more energy, be it by lower swimming performance or by requiring more attempts to successfully cross the passages. Studying variation in hydrodynamic morphology can thus provide a useful tool for developing the most appropriate passageways.

In light of hydrodynamics, electronic devices such as pop-off satellite archival tags and data storage tags are increasingly applied to gain fundamental insight in silver eel migration behavior in the marine environment (Hussey et al. 2015). These devices are externally attached to the eel's body and therefore might interfere with its hydrodynamic shape and performance (Tudorache et al. 2014). Hence, morphology-focused studies could aid this fundamental research field to fine tune tagging protocols and to draw correct conclusions from the obtained data (e.g. biased swim speeds by tag interference), indirectly contributing to eel management.

## Conclusions

A lot more conservation measures and efforts are necessary in order to restore the European eel population to healthy levels. Functional morphological studies are generally given less attention in terms of developing conservation plans. However, the above listed studies show that insight in morphological variation and its link with performance and habitat use might be crucial to develop effective management measures.

## Funding

This work was supported by the Special Research Fund (BOF; PDO.2017.001.301 Fund IV1).

## References

Arnold SJ. 1983. Morphology, performance, and fitness. Am Zool 23:347–61.

Arnold SJ. 2003. Performance surfaces and adaptive landscapes. Integr Comp Biol 43:367–75.

Bark A, Williams B, Knights B. 2007. Current status and temporal trends in stocks of European eel in England and Wales. ICES J Mar Sci 64:1368–78.

Barry J, Mcleish J, Dodd JA, Turnbull JF, Boylan P, Adams CE. 2014. Introduced parasite *Anguillicola crassus* infection significantly impedes swim bladder function in the European eel *Anguilla anguilla* (L.). J Fish Dis 37:921–4.

Barry J, Newton M, Dodd JA, Hooker OE, Boylan P, Lucas MC, Adams CE. 2016. Foraging specialisms influence space use and movement patterns of the European eel *Anguilla anguilla*. Hydrobiologia 766:333–48.

Belpaire C, Goemans G. 2007. The European eel *Anguilla anguilla*, a rapporteur of the chemical status for the water framework directive?. Life Environ 57:235–52.

Belpaire C, Pujolar JM, Geeraerts C, Maes GE. 2016. Contaminants in eels and their role in the collapse of the eel stocks. In: Arai T, editor. Biology and ecology of anguillid eels. Boca Raton (FL): CRC Press - Taylor & Francis Group. p. 225–50.

Christoffersen M, Svendsen JC, Kuhn JA, Nielsen A, Martjanova A, Stottrup JG. 2018. Benthic habitat selection in juvenile European eel *Anguilla anguilla*: implications for coastal habitat management and restoration. J Fish Biol 93:996–9.

Cooper WE, Vitt LJ. 1993. Female mate choice of large male broad-headed skinks. Anim Behav 45:683–93.

Cucherousset J, Acou A, Blanchet S, Britton JR, Beaumont WRC, Gozlan RE. 2011. Fitness consequences of individual specialisation in resource use and trophic morphology in European eels. Oecologia 167:75–84.

Dainys J, Stakėnas S, Gorfine H, Ložys L. 2018. Mortality of silver eels migrating through different types of hydropower turbines in Lithuania. River Res Appl 34:52–9.

de Groot SJ. 1996. The physical impact of marine aggregate extraction in the North Sea. ICES J Mar Sci 53:1051–3.

De Meyer J, Belpaire C, Boeckx P, Bervoets L, Covaci A, Malarvannan G, De Kegel B, Adriaens D. 2018a. Head shape disparity impacts pollutant accumulation in European eel. Environ Pollut 240:378–86.

De Meyer J, Christiaens J, Adriaens D. 2016. Diet-induced phenotypic plasticity in European eel (*Anguilla anguilla*). J Exp Biol 219:354–63.

De Meyer J, Goethals T, Van Wassenbergh S, Augustijns T, Habraken J, Hellemans J, Vandewiele V, Dhaene J, Bouillart M, Adriaens D. 2018b. Dimorphism throughout the European eel's life cycle: are ontogenetic changes in head shape related to dietary differences? J Anat

De Meyer J, Herrel A, Belpaire C, Goemans G, Ide C, De Kegel B, Christiaens J, Adriaens D. 2018c. Broader head, stronger bite: *in vivo* bite forces in European eel *Anguilla anguilla*. J Fish Biol 92:268–73.

De Meyer J, Maes GE, Dirks RP, Adriaens D. 2017. Differential gene expression in narrow- and broad-headed European glass eels (*Anguilla anguilla*) points to a transcriptomic link of head shape dimorphism with growth rate and chemotaxis. Mol Ecol 26:3943–53.

De Meyer J, Van Wassenbergh S, Bouilliart M, Dhaene J, Adriaens D. 2018d. Built to bite? Differences in cranial morphology and bite performance between narrow- and broad-headed European glass eels. J Morphol 279:349–60.

Dekker W, Van Os B, Van Willigen J. 1998. Minimal and maximal size of eel. Bull Fr Pêche Piscic 349:195–7.

Desprez M. 2000. Physical and biological impact of marine aggregate extraction along the French coast of the Eastern English Channel: short and long-term post-dredging restoration. ICES J Mar Sci 57:1428–38.

Domenici P. 2001. The scaling of locomotor performance in predator–prey encounters: from fish to killer whales. Comp Biochem Physiol A Mol Integr Physiol 131:169–82.

Drouineau H, Durif C, Castonguay M, Mateo M, Rochard E, Verreault G, Yokouchi K, Lambert P. 2018. Freshwater eels: a symbol of the effects of global change. Fish Fish (Oxf) 19:903–30.

Egg L, Mueller M, Pander J, Knott J, Geist J. 2017. Improving European Silver Eel (*Anguilla anguilla*) downstream migration by undershot sluice gate management at a small-scale hydropower plant. Ecol Eng 106:349–57.

Fjeldstad H-P, Pulg U, Forseth T. 2018. Safe two-way migration for salmonids and eel past hydropower structures in Europe: a review and recommendations for best-practice solutions. Mar Freshw Res 69:1834.

Foekema EM, Kotterman M, de Vries P, Murk AJ. 2016. Maternally transferred dioxin-like compounds can affect the reproductive success of European eel. Environ Toxicol Chem 35:241–6.

Freyhof J, Brooks E. 2011. European red list of freshwater species. Luxembourg: Publications Office of the European Union.

Gage JD, Roberts JM, Hartley JP, Humphery JD. 2005. Potential impacts of deep-sea trawling on the benthic ecosystem along the northern European continental margin: a review. In: Barnes PW, Thomas JP, editors. American fisheries society symposium 41: benthic habitats and the effects of fishing. Bethesda (MD): American Fisheries Society. p. 503–17.

Geeraerts C, Belpaire C. 2010. The effects of contaminants in European eel: a review. Ecotoxicology 19:239–66.

Heisey PG, Mathur D, Phipps JL, Avalos JC, Hoffman CE, Adams SW, De-Oliveira E. 2019. Passage survival of European and American eels at Francis and propeller turbines. J Fish Biol 95:1172–83.

Herrel A, Choi HF, Dumont E, De Schepper N, Vanhooydonck B, Aerts P, Adriaens D. 2011. Burrowing and subsurface locomotion in anguilliform fish: behavioral specializations and mechanical constraints. J Exp Biol 214:1379–85.

Herrel A, Meyers JJ, Vanhooydonck B. 2001. Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. Biol J Linn Soc Lond 74:305–14.

Holland LE. 1986. Effects of barge traffic on distribution and survival of ichthyoplankton and small fishes in the Upper Mississippi River. Trans Am Fish Soc 115:162–5.

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, et al. 2015. Aquatic animal telemetry: a panoramic window into the underwater world. Science 348:1255642.

ICES. 2016. Report of the working group on the effects of extraction of marine sediments on the marine ecosystem (WGEXT). Gdansk: ICES CM.

Ide C, De Schepper N, Christiaens J, Van Liefferinge C, Herrel A, Goemans G, Meire P, Belpaire C, Geeraerts C, Adriaens D. 2011. Bimodality in head shape in European eel. J Zool 285:230–8.

Irschick DJ. 2003. Measuring performance in nature: implications for studies of fitness within populations. Integr Comp Biol 43:396–407.

Jacoby D, Gollock M. 2014. *Anguilla anguilla*. The IUCN red list of threatened species: e.T60344A45833138.

Jellyman PG, Bauld JT, Crow SK. 2017. The effect of ramp slope and surface type on the climbing success of shortfin eel (*Anguilla australis*) elvers. Mar Freshw Res 68:1317.

Johnson LJ, Misitano D, Sol SY, Nelson GM, French B, Ylitalo GM, Hom T. 1998. Contaminant effects on ovarian development and spawning success in rock sole from Puget Sound, Washington. Trans Am Fish Soc 127:375–92.

Kennedy CR. 2007. The pathogenic helminth parasites of eels. J Fish Dis 30:319–34.

Kirk RS. 2003. The impact of *Anguillicola crassus* on European eels. Fish Manage Ecol 10:385–94.

Knopf K, Mahnke M. 2004. Differences in susceptibility of the European eel (*Anguilla anguilla*) and the Japanese eel (*Anguilla japonica*) to the swim-bladder nematode *Anguillicola crassus*. Parasitology 129:491–6.

Lammens EH, Visser JT. 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.

Lappin AK, Husak JF. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). Am Nat 166:426–36.

Lefebvre F, Fazio G, Mounaix B, Crivelli AJ. 2013. Is the continental life of the European eel *Anguilla anguilla* affected by the parasitic invader *Anguillicoloides crassus*?. Proc Biol Sci 280:20122916.

Legault A. 1992. Étude de quelques facteurs de sélectivité de passes à anguilles. Bull Fr Pêche Piscic 83–91.

Legault A, Fontenelle G, Gascuel D, Rigaud C. 1990. Eel ladder devices in Europe. Int Rev Hydrobiol 75:843–4.

Losos JB. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. Berkely and Los Angeles (CA): University of California Press.

Neto AF, Costa JL, Costa MJ, Domingos I. 2010. Epidemiology and pathology of *Anguillicoloides crassus* in European eel *Anguilla anguilla* from the Tagus estuary (Portugal). Dis Aquat Organ 88:225–33.

Nzau Matondo B, Séleck E, Dierckx A, Benitez JP, Rollin X, Ovidio M. 2019. What happens to glass eels after restocking in upland rivers? A long-term study on their dispersal and behavioural traits. Aquat Conserv 29:374–88.

Okland F, Teichert MAK, Havn TB, Thorstad EB, Heermann L, Saether SA, Thambets M, Borcherding J. 2017. Downstream migration of European eel at three German hydropower stations. NINA Report 1355:1–53.

Palstra A, van Ginneken V, van den Thillart G. 2008. Cost of transport and optimal swimming speed in farmed and wild European silver eels (*Anguilla anguilla*). Comp Biochem Physiol A Mol Integr Physiol 151:37–44.

Palstra AP, Heppener DFM, van Ginneken VJT, Székely C, van den Thillart G. 2007. Swimming performance of silver

eels is severely impaired by the swim-bladder parasite *Anguillicola crassus*. J Exp Mar Biol Ecol 352:244–56.
Pedersen MI, Rasmussen GH. 2018. Fisheries regulation on European eel (*Anguilla anguilla*) for 2018; how big is the effect?. J Fish Res 2:17–8.
Pegg J, Andreou D, Williams CF, Britton JR. 2015. Head morphology and piscivory of European eels, *Anguilla anguilla*, predict their probability of infection by the invasive parasitic nematode *Anguillicoloides crassus*. Freshw Biol 60:1977–87.
Pelster B. 2015. Swimbladder function and the spawning migration of the European eel *Anguilla anguilla*. Front Physiol 5:486.
Petterson IJ. 2019. Evaluating substrate preference in juvenile European eels (Anguilla anguilla) for aquatic habitat restoration. Lund: Lund University.
Piper AT, Svendsen JC, Wright RM, Kemp PS. 2017. Movement patterns of seaward migrating European eel (*Anguilla anguilla*) at a complex of riverine barriers: implications for conservation. Ecol Freshw Fish 26:87–98.
Proman JM, Reynolds JD. 2000. Differences in head shape of the European eel, *Anguilla anguilla* (L.). Fish Manage Ecol 7:349–54.
Robinet T, Feunteun E. 2002. Sublethal effects of exposure to chemical compounds: a cause for the decline in Atlantic eels? Ecotoxicology 11:265–77.
Schoenfuss HL, Blob RW. 2007. The importance of functional morphology for fishery conservation and management: applications to Hawaiian amphidromous fishes. Bishop Mus Bull Cult Environ Stud 3:125–41.
Simon J. 2007. Age, growth, and condition of European eel (*Anguilla anguilla*) from six lakes in the River Havel system (Germany). ICES J Mar Sci 64:1414–22.
Simon J, Westerberg H, Righton D, Sjöberg NB, Dorow M. 2018. Diving activity of migrating silver eel with and without *Anguillicola crassus* infection. J Appl Ichthyol 34:659–68.
Steendam C. 2019. The burrowing eel: effects of life stage and head shape. [Master's thesis]: University of Ghent. p. 1–79.
Stein F, Doering-Arjes P, Fladung E, Brämick U, Bendall B, Schröder B. 2016. Downstream migration of the European Eel (*Anguilla Anguilla*) in the Elbe River, Germany: movement patterns and the potential impact of environmental factors. River Res Appl 32:666–76.
Sures B, Streit B. 2001. Eel parasite diversity and intermediate host abundance in the River Rhine, Germany. Parasitology 123:185–91.
Szekely B. 1994. Paratenic hosts for the parasitic nematode *Anguillicola crassus* in Lake Balaton. Hungary. Dis Aquat Organ 18:11–20.
Tamario C, Calles O, Watz J, Nilsson PA, Degerman E. 2019. Coastal river connectivity and the distribution of ascending juvenile European eel (*Anguilla anguilla* L.): implications for conservation strategies regarding fish-passage solutions. Aquat Conserv 29:612–22.
Teodecki EE, Brodie ED, Formanowicz DR, Nussbaum RA. 1998. Head dimorphism and burrowing speed in the African Caecilian *Schistometopum thomense* (Amphibia: Gymnophiona). Herpetologica 54:154–60.
Tesch FW. 2003. The eel. Oxford: Blackwell Science.
Thurow F. 1958. Untersuchungen uber die spitz und breitköpfigen Varianten des Flussaales. Arch Fisch 9:79–97.
Törlitz H. 1922. Anatomische und entwicklungsgeschichtliche Beiträge zur Artfrage unseres Flussaales. Z Fisch 21:1–48.
Tudorache C, Burgerhout E, Brittijn S, Van den Thillart G. 2014. The effect of drag and attachment site of external tags on swimming eels: experimental quantification and evaluation tool. PLoS One 9:e112280.
Tytell ED. 2004. The hydrodynamics of eel swimming II. Effect of swimming speed. J Exp Biol 207:3265–79.
Tytell ED, Lauder GV. 2004. The hydrodynamics of eel swimming I. Wake structure. J Exp Biol 207:1825–41.
van den Thillart G, van Ginneken V, Körner F, Heijmans R, van der Linden R, Gluvers A. 2004. Endurance swimming of European eel. J Fish Biol 65:312–8.
van Ginneken V, Antonissen E, Müller UK, Booms R, Eding E, Verreth J, van den Thillart G. 2005. Eel migration to the Sargasso: remarkably high swimming efficiency and low energy costs. J Exp Biol 208:1329–35.
Van Wassenbergh S, Brecko J, Aerts P, Stouten I, Vanheusden G, Camps A, Van Damme R, Herrel A. 2010. Hydrodynamic constraints on prey-capture performance in forward-striking snakes. J Royal Soc Interface 7:773–85.
Van Wassenbergh S, Potes NZ, Adriaens D. 2015. Hydrodynamic drag constrains head enlargement for mouthbrooding in cichlids. J Royal Soc Interface 12:20150461.
Vanhooydonck B, Boistel R, Fernandez V, Herrel A. 2011. Push and bite: trade-offs between burrowing and biting in a burrowing skink (*Acontias percivali*). Biol J Linn Soc 102:91–9.
Verhelst P, Buysse D, Reubens J, Pauwels I, Aelterman B, Van Hoey S, Goethals P, Coeck J, Moens T, Mouton A. 2018. Downstream migration of European eel (*Anguilla anguilla* L.) in an anthropogenically regulated freshwater system: implications for management. Fish Res 199:252–62.
Verhelst P, De Meyer J, Reubens J, Coeck J, Goethals P, Moens T, Mouton A. 2018. Unimodal head-width distribution of the European eel (*Anguilla anguilla* L.) from the Zeeschelde does not support disruptive selection. PeerJ 6:e5773.
Vogel S. 1994. Life in moving fluids: the physical biology of flow. Princeton (NJ): Princeton University Press.
Walters V. 1962. Body form and swimming performance in the Scombroid fishes. Am Zool 2:143–9.
Watz J, Nilsson PA, Degerman E, Tamario C, Calles O. 2019. Climbing the ladder: an evaluation of three different anguillid eel climbing substrata and placement of upstream passage solutions at migration barriers. Anim Conserv 22:452–62.
Webb PW. 1984. Form and function in fish swimming. Sci Am 251:72–83.
Winter H, Jansen H, Bruijs M. 2006. Assessing the impact of hydropower and fisheries on downstream migrating silver eel, *Anguilla anguilla*, by telemetry in the River Meuse. Ecol Freshw Fish 15:221–8.
Wolter C, Arlinghaus R. 2003. Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance. Rev Fish Biol Fish 13:63–89.