

# Fitness consequences of individual specialisation in resource use and trophic morphology in European eels

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**Abstract** Individual specialisation can lead to the exploitation of different trophic and habitat resources and the production of morphological variability within a population. Although the ecological causes of this phenomenon are relatively well known, its consequences on individual fitness are less recognised. We have investigated the extent of individual specialisation in resource use and trophic morphology and its fitness consequences through a combination of tagging–recapture, stable isotope analyses and telemetry. The European eel (*Anguilla anguilla*) was

the model species as it displays significant variability in head shape. Independent to their body length, individuals with broader heads displayed a significantly higher trophic position ( $\delta^{15}\text{N}$ ) than individuals with narrower heads. This corresponded with a significantly higher proportion of prey fish in their diet compared with invertebrates and was associated with the use of a habitat niche located further from the river bank. The European eel therefore provides a rare empirical example of individual specialisation in resource use and trophic morphology in a natural population occurring at a very small spatial scale. Individuals with intermediate head morphology displayed lower body condition (a proxy of fitness) than individuals with extreme head morphology (i.e. narrower and broader headed individuals), demonstrating the existence of disruptive selection associated with individual specialisation.

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## Introduction

Individuals within populations behave to maximise their fitness, notably by optimising energy acquisition, and where food resources are scarce, this can drive individual specialisation (Bolnick et al. 2003). Such specialisation may lead to variation in the phenotypic characters of individuals that relate to the exploitation of habitat and/or trophic resources and can result in the development of variable morphological traits. When individual specialisation leads to the occurrence of discrete morphs, the process is commonly referred to as trophic or resource polymorphism (Skulason and Smith 1995; Smith and Skulason

1996; Ward et al. 2006). This is believed to be a key intermediate step underpinning speciation (Smith and Skulason 1996) and is thought to be driven by intraspecific competition through increased density and/or decreased resource availability (Mittelbach et al. 1992; Skulason and Smith 1995; Smith and Skulason 1996). Competition strength is reduced as individual specialisation enables the exploitation of alternative resources within the population (Bolnick et al. 2003; Swanson et al. 2003; Svanbäck and Bolnick 2007). In turn, ecological feedbacks, such as resource availability and predation pressure, regulate individual specialisation (e.g. Rundle et al. 2003; Svanbäck and Persson 2004; Andersson et al. 2007).

Despite our understanding of the drivers behind ecological specialisation, its consequences on individual fitness are generally less recognised. Morphological variability is produced mainly by the interplay between the individual genotype and the environment (Skulason and Smith 1995; Bolnick et al. 2003; Proulx and Magnan 2004), and it is expected that phenotypes coexist with different fitness values. For instance, disruptive selection is important to maintain resource polymorphism (Smith and Skulason 1996; Martin and Pfennig 2009), and theory and recent field investigations suggest that disruptive selection should increase phenotypic variability as individuals with intermediate traits have fitness disadvantages compared to coexisting individuals with more extreme traits (e.g. Bolnick 2004; Carlson et al. 2007; Martin and Pfennig 2009). Therefore, the question of the fitness consequences of individual specialisation is central to predicting the evolutionary trajectories of populations subjected to it.

In many of the species in which head morphology limits energy acquisition, such as amphibians, reptiles, birds and fish (Smith and Skulason 1996; Bulté et al. 2008), differences in head morphology have direct implications for individual foraging efficiency and resource acquisition, including capture, handling and gape-limitations (Hori 1993; Ward et al. 2006; Svanbäck and Bolnick 2008). Indeed, increased gape-size enables individuals to consume larger prey and potentially obtain higher energy returns (e.g. Galarowicz and Wahl 2005). It is then expected that intrapopulation differences in head morphology may lead to higher fitness in individuals more able to consume profitable prey (Bulté et al. 2008). However, a trade-off between foraging performance and trophic morphology can occur in which individuals with intermediate trophic morphology may be less efficient than those with extreme trophic morphology, i.e. extreme morphologies optimise the foraging performance for each alternative trophic resource (Martin and Pfennig 2009).

To characterise the consequences of specialisation in resource use and trophic morphology on individual fitness in wild populations, we used the European eel (*Anguilla*

*anguilla* L.) as the model species. Within populations, eels can show considerable variation in habitat use (e.g. Harrod et al. 2005) and head width (Tesch 2003). Although this polymorphism has resulted in dichotomous descriptions of ‘broad-headed individuals’ and ‘narrow-headed individuals’ (Lammens and Visser 1989; Provan and Reynolds 2000; Tesch 2003), this distinction is debatable as the differences may instead represent continuous morphological variation. Moreover, it remains unclear if morphological variations in eel are associated with habitat and/or trophic niche differences, and if they affect individual fitness. Consequently, we used a combination of individual tagging, portable telemetry and stable isotope analyses to test the following hypotheses: (1) head-shape variability in the eel is associated with trophic and/or habitat niche segregation; (2) this variability results in unequal fitness between individuals (using body condition as a fitness proxy, e.g. Jakob et al. 1996; Bulté et al. 2008). We predicted that (1) individuals with broader heads would display a higher trophic position than individuals with narrower heads due to a higher proportion of prey fish (as opposed to invertebrates) in their diet and utilise different habitats (Svanbäck and Eklöv 2002; Dörner et al. 2009; Quevedo et al. 2009), and (2) extreme trophic morphology (i.e. narrower and broader headed individuals) would display higher body condition (fitness) than intermediate trophic morphology (e.g. Martin and Pfennig 2009).

## Materials and methods

### Study area and population monitoring

The study was conducted in a 520-m length of a side channel of the River Frome, UK (50°40′4″N; 2°10′42″W). The study commenced on 17 July 2008 when the fish were initially captured by electric fishing (details in Cucherousset et al. 2010). Captured individuals were anaesthetised with 2-phenoxyethanol, measured [total length (TL), nearest millimetre] and weighed [weight (W), nearest 0.1 g]. Among the 117 individuals captured whose TL was >300 mm, we included a random sub-sample of 60 individuals in the study. For each individual, head width (HW, nearest 0.1 mm) was measured between the outside of the jaw hinges using a calliper (Provan and Reynolds 2000), a 12-mm passive integrated transponder (PIT) tag was inserted into the peritoneal cavity using a sterile scalpel and a fin-clip was taken for stable isotope analyses. After being allowed to recover in oxygenated water, the eels were released back into the reach where they were sampled.

Using the same sampling protocol, electric fishing was conducted on 18 August 2008, 23 September 2008 and 10

October 2008 in order to recapture individuals over a 3-month period (hereafter referred to as the ‘short-term period’). Each eel captured was checked for a PIT-tag; recaptured individuals were anaesthetised with 2-phenoxyethanol, measured, weighed and fin-clipped before being released. In total 15, 10 and 11 individuals were recaptured in August, September and October 2008, respectively. Among these, ten individuals were recaptured twice. To avoid pseudo-replication in further analyses, we only used the data collected from their last recapture; therefore, the short-term period dataset consisted of 26 individuals (i.e. 43% of tagged individuals). Electric fishing was repeated on 10 July 2009 (hereafter referred to as the ‘long-term period’), and the same procedure (without fin-clipping) was applied. A total of 13 individuals (i.e. 20% of tagged individuals) were recaptured and subsequently released back into the study area. Data from a total of 99 capture–recapture events were collected.

### Trophic niche

The fin samples collected at tagging and over the short-term period were subjected to stable isotope analyses ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) to quantify the trophic niche. This tissue was selected as stable isotopes in the fin correlate closely with those of muscle tissue in many fishes, and this procedure enables non-lethal sampling (Jardine et al. 2005; Syväranta et al. 2010). Additionally, samples of potential prey items were collected to quantify their contribution to eel diet, including the most abundant invertebrates (four families: Brachycentridae, Gammaridae, Limnephilidae and Neritidae) and prey fish (minnow *Phoxinus phoxinus* and dace *Leuciscus leuciscus*). Prey samples were collected during the tagging period (June–July) and throughout the short-term period (August–October) to include any potential seasonal changes in prey stable isotope values. Invertebrate and minnow samples were composed of pooled samples ( $n = 2$ –19 individuals per sample). A portion of foot muscle and dorsal muscle was dissected from Neritidae and prey fish respectively, while whole specimens of other organisms were analysed. Samples were processed according to the procedure described by Syväranta et al. (2010) and analysed at the Stable Isotopes in Nature Laboratory, University of New Brunswick, New Brunswick, Canada.

### Habitat niche

Two days before the start of the monitoring, the study area was divided into 73 cells of approximately 20–30 m<sup>2</sup> to determine eel habitat use at the meso-habitat (between cells) and micro-habitat (within cell) scales. For each cell, three meso-habitat variables were measured: channel width

(metres), vegetation cover (%) and substratum characteristics. The substrate score in each cell was subsequently calculated according to grain size (0 = silt, 1 = sand, 2 = gravel, 3 = cobble, 4 = pebble). At the micro-habitat scale, water depth (centimetre) and flow velocity (centimetre per second) were measured at 25, 50 and 75% of the channel width in each cell. Eel locations were determined using a portable PIT detector to localise tagged individuals without the need of handling (Cucherousset et al. 2005). Twenty-five tracking surveys were completed between 23 July 2008 and 9 October 2008 (approximately two per week), all performed by the same operator; each survey lasted on average 3.5 h and commenced at dawn, mid-day or dusk. When a tagged eel was detected, cell identity and the distance to the closest bank (nearest 0.1 m) were recorded (details on tracking in Cucherousset et al. 2010). To ensure that habitat niche assessment was not biased by tag loss, only data on those localisations that were followed by a recapture during any of the electric fishing surveys were used. Among the 60 PIT-tagged individuals, 22 individuals were localised at least once before being recaptured and, on average, each individual was localised on 4.5 occasions [ $\pm 3.4$  standard deviation (SD)]. Data on a total of 99 individual localisations followed by recapture were used for further analyses.

### Data analyses

Following Provan and Reynolds (2000), the ratio HW:TL was calculated for each individual at tagging and subsequently used as a morphological index. Independent of their TL, individuals with higher values of morphological index had broader heads. After inspection of normality, linear regression was used to test whether the morphological index (HW:TL) was correlated to TL (log-transformed).

### Trophic and habitat niches

According to the structure of the dataset (i.e. individuals recaptured several times at different periods) and since TL was correlated to the morphological index, differences in trophic and habitat niches between individuals were investigated using mixed linear models. The models were built using each trophic niche variable (i.e.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) as the response variable, each individual capture or recapture as the replicate unit ( $n = 85$ ) and individual identity as the random variable. Each model was initially fitted with TL (log-transformed), HW:TL, period (tagging and short-term) and the interactions terms period  $\times$  HW:TL and period  $\times$  TL as fixed predictors and, subsequently, without the interaction terms when they were not significant.

A mixing model approach was then used to determine the contribution of each potential prey item to the diet of each tagged individual. The Stable Isotope Analysis in R package (SIAR, Parnell et al. 2008) was used as it accounts for variability in the isotopic values of consumers, prey and trophic fractionation (Parnell et al. 2010). The models were run separately at the individual level for the two periods (i.e. tagging and short-term) since a significant effect of 'period' on stable isotope values was detected (see below). For each period, five potential prey items were used: three invertebrate families (for the tagging period: Brachycentridae  $n = 1$ , Gammaridae  $n = 6$ , Limnephilidae  $n = 4$ ; for the short-term period: Brachycentridae  $n = 3$ , Gammaridae  $n = 5$ , Neritidae  $n = 2$ ) and two fish species (dace  $n = 1$  and  $n = 6$ , respectively; minnow  $n = 5$  and  $n = 9$ , respectively). For each potential prey item and for each period, the average and standard deviation of potential prey items were used in the mixing models. As there is no specific trophic fractionation factor for eels available in the literature, the approach of Inger et al. (2010) was used where the values in the mixing model were averaged trophic fractionation factors reported in the literature (e.g. Post 2002) with a large standard deviation. Thus, we used a fractionation of 1.0‰ ( $\pm 1.0$  SD) and 3.3‰ ( $\pm 1.0$  SD) for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively (Inger et al. 2010). The mean contribution of prey fish to the diet of each individual was then calculated by summing the mean contributions of minnow and dace. We then tested the effect of the morphological index on the mean contribution of prey fish to the diet of each individual using a mixed linear model (same model structure as described but with the mean contribution of prey fish as a response variable).

A similar statistical approach was used to test the effects of the morphological index on the habitat niche. The models were built using each habitat niche variable (i.e. river width, substrate score, vegetation cover, distance to the bank, water velocity and water depth) as the response variable, each individual localisation as the replicate unit ( $n = 99$ ) and individual identity as the random variable. Each model was initially fitted with TL (log-transformed), HW:TL and the interaction term TL  $\times$  HW:TL as a fixed predictor and, subsequently, without the interaction term when it was not significant. No period effect was tested since all habitat niche data were collected during the short-term period.

### Body condition

In many animals, body condition is a strong proxy of fitness (e.g. Jakob et al. 1996; Bulté et al. 2008). In eel, it is correlated with individual quality prior to transoceanic migration (as energy reserves strongly affect swimming capability) and gonado-somatic index (Tesch 2003; Durif

et al. 2005; EELREP 2005) and positively related to fat content (e.g. Van Ginneken et al. 2007; Belpaire et al. 2008). Thus, body condition is a good surrogate of eel individual fitness, especially in studies in which individuals are not sacrificed. The effect of the morphological index on individual body condition was tested using a mixed linear model to account for the structure of the dataset, for eel growth not being isometric and for body condition being correlated to TL (e.g. Acou et al. 2008). The model was built using W (log-transformed) as the response variable, each capture or recapture as the replicate unit ( $n = 99$ ) and individual identity as the random variable. The model was initially fitted with TL (log-transformed), HW:TL, period (tagging, short-term and long-term) and their interactions terms, period  $\times$  TL (log-transformed) and period  $\times$  HW:TL, respectively, as fixed descriptors. The initial model also included the quadratic term of the morphological index (HW:TL)<sup>2</sup> and its interaction term with period as an additional fixed predictor to test whether body condition was, as predicted, a quadratic function (curvilinear and U-shaped) of the morphological index (e.g. Bolnick 2004). The model was subsequently run without the interaction terms when they were not significant. Following Lande and Arnold (1983), fixed predictors were transformed to Z scores to obtain standardised slope estimates ( $\beta$ ). All statistical analyses were performed using R (R Development Core Team 2007).

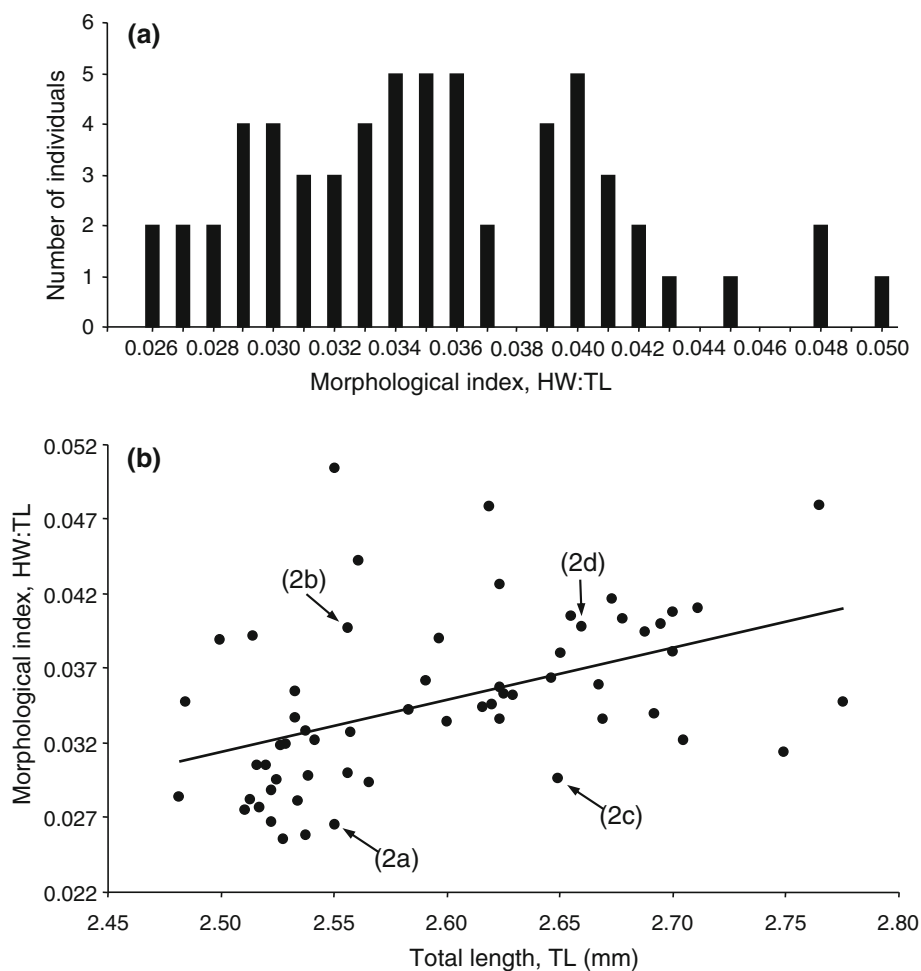
### Results

Among the 60 individuals initially PIT-tagged [mean  $\pm$  SD: TL 401.9  $\pm$  73.4 mm; W 138.8  $\pm$  94.0 g), the morphological index (HW:TL) averaged 0.035  $\pm$  0.006, ranged from 0.026 to 0.050 (Fig. 1a) and significantly increased as TL increased (linear regression  $a = 0.035$ ,  $b = -0.056$ ,  $r^2 = 0.22$ ,  $p < 0.001$ ,  $n = 60$ ; Fig. 1b). Some individuals of the same TL also had different morphological index values (Figs. 1b, 2).

### Trophic and habitat niches

$\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  increased as TL increased, while significant effects of period were observed for  $\delta^{15}\text{N}$  (Table 1). Independent of TL and period,  $\delta^{15}\text{N}$  was positively correlated with the morphological index, where eels with broader heads were significantly  $^{15}\text{N}$ -enriched compared to individuals with narrower heads (Table 1, Fig. 3a–d). No significant relationship between the morphological index and  $\delta^{13}\text{C}$  was found. Using the stable isotope values ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) of eels and their potential prey items, the mixing models revealed that the mean contribution of prey fish in the eel diet ranged from 26.7 to 82.0%. The contribution of

**Fig. 1** **a** Distribution of the morphological index [ $HW:TL$  ratio; i.e. ratio of head width ( $HW$ , mm) to total length ( $TL$ , mm)] among the 60 individually tagged European eels (*Anguilla anguilla*), **b** relationship between the morphological index ( $HW:TL$  ratio) and  $TL$  (log-transformed) for eels at tagging ( $n = 60$ ). The regression line is significant (linear regression  $a = 0.035$ ,  $b = -0.056$ ,  $r^2 = 0.22$ ,  $p < 0.001$ ). Arrows indicate datapoints of four individuals whose pictures are displayed in Fig. 2



prey fish to the eel diet increased with  $TL$  and differed between periods (Table 1, Fig. 3e, f). Independent of  $TL$  and period, the contribution of prey fish to diet was positively correlated with the morphological index where broader headed eels consumed a significantly higher proportion of prey fish than individuals with narrower heads (Table 1, Fig. 3e, f).

There was a positive and significant correlation between the morphological index ( $HW:TL$ ) and the distance to the bank, while there was no significant correlation between the morphological index and any of the other micro- and meso-habitat variables (Table 2). Therefore, individuals with narrower heads (i.e. lower morphological index) occupied a habitat niche nearer to the bank than individuals with broader heads.

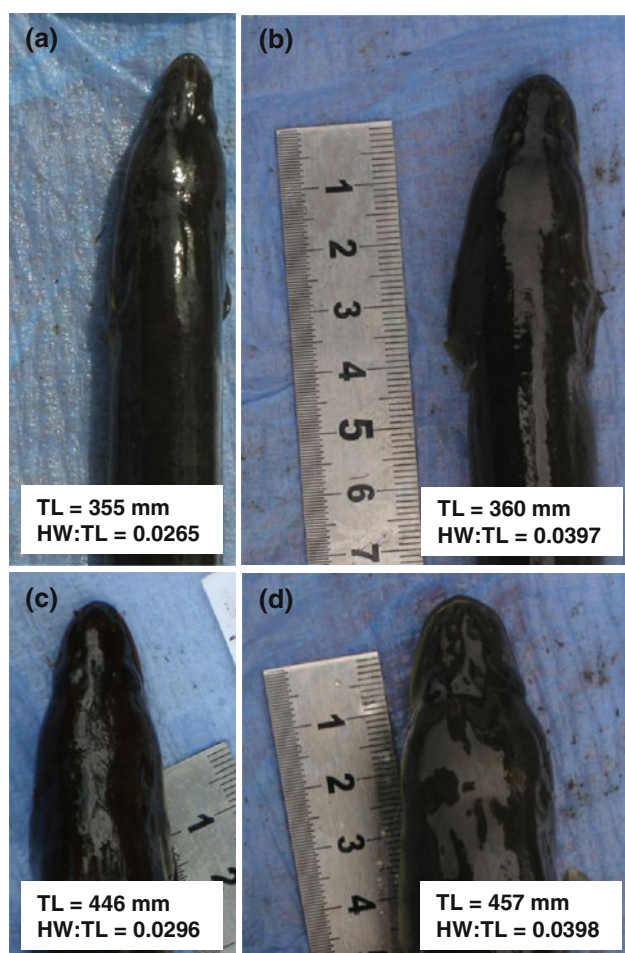
#### Body condition

The body condition of eels was positively correlated to  $TL$  and differed between periods (Table 3). However, independent of  $TL$  and period, there was a significant curvilinear and U-shaped relationship between body condition

and the morphological index since both the simple and quadratic terms of the morphological index were significant (Table 3). As predicted, individuals with intermediate morphological index values displayed lower body conditions than individuals with extreme morphological index values (i.e. narrower and broader headed individuals; Fig. 4).

#### Discussion

The results of this study indicated that morphological variability in eel head shape was associated with inter-individual variability in trophic and habitat niches and that it induced unequal fitness between individuals. There was strong evidence that decreased morphological index values induced a lower trophic position and a habitat niche nearer to the river bank, and vice versa. Eels with different head widths displayed significant patterns of trophic niche segregation that were consistent over time. These findings support those of previous studies which used analyses of stomach contents for demonstrating that an increased



**Fig. 2** Small-bodied eels with narrower (a) and broader (b) heads and large-bodied eels with narrower (c) and broader (d) heads. TL and HW:TL are shown for each individual

HW:TL ratio induced an increased consumption of larger and/or harder prey (Lammens and Visser 1989; Provan and Reynolds 2000). The differences in  $\delta^{15}\text{N}$  among individuals with different morphological index values and similar TL indicated that these individuals were less than a trophic position apart (e.g. Post 2002), suggesting that the broader headed individuals did not display exclusive piscivory (e.g. Dörner et al. 2009). Although differences of approximately one trophic position between individuals belonging to different morphotypes have been observed in other species (e.g. McCarthy et al. 2004), such studies are generally performed at relatively large spatial scales and, in fish, most examples relate to lake populations where morphological groups segregate over discrete habitats, such as littoral/benthic versus pelagic habitats (e.g. Svanbäck and Eklöv 2002; Proulx and Magnan 2004; Quevedo et al. 2009). By contrast, this study was performed at a much smaller spatial scale in an area of relatively low level of habitat heterogeneity, a situation observed in many riverine ecosystems where examples are relatively scarce

**Table 1** Results of the mixed linear models used to test for the effects of the morphological index (HW:TL) on the trophic niche of European eels ( $n = 85$ )

Parameter <sup>a</sup>	Source of variation	df	Estimate (SE)	<i>p</i>
$\delta^{15}\text{N}$	TL	24	2.17 (0.46)	<0.001***
	Period	24	0.42 (0.08)	<0.001***
	HW:TL	57	31.28 (14.18)	0.031*
	Intercept	57	0.74 (2.53)	0.771
$\delta^{13}\text{C}$	TL	24	1.23 (0.35)	0.002**
	Period	24	-0.038 (0.09)	0.669
	HW:TL	57	-17.48 (11.05)	0.119
	Intercept	57	-35.18 (1.96)	<0.001***
Prey fish	TL	24	0.30 (0.06)	<0.001***
	Period	24	0.05 (0.01)	<0.001***
	HW:TL	57	4.26 (1.93)	0.032*
	Intercept	57	-1.42 (0.34)	<0.001***

TL, Total length (mm); HW, head width (mm); HW:TL, morphological index (i.e. ratio of HW to TL); SE, standard error

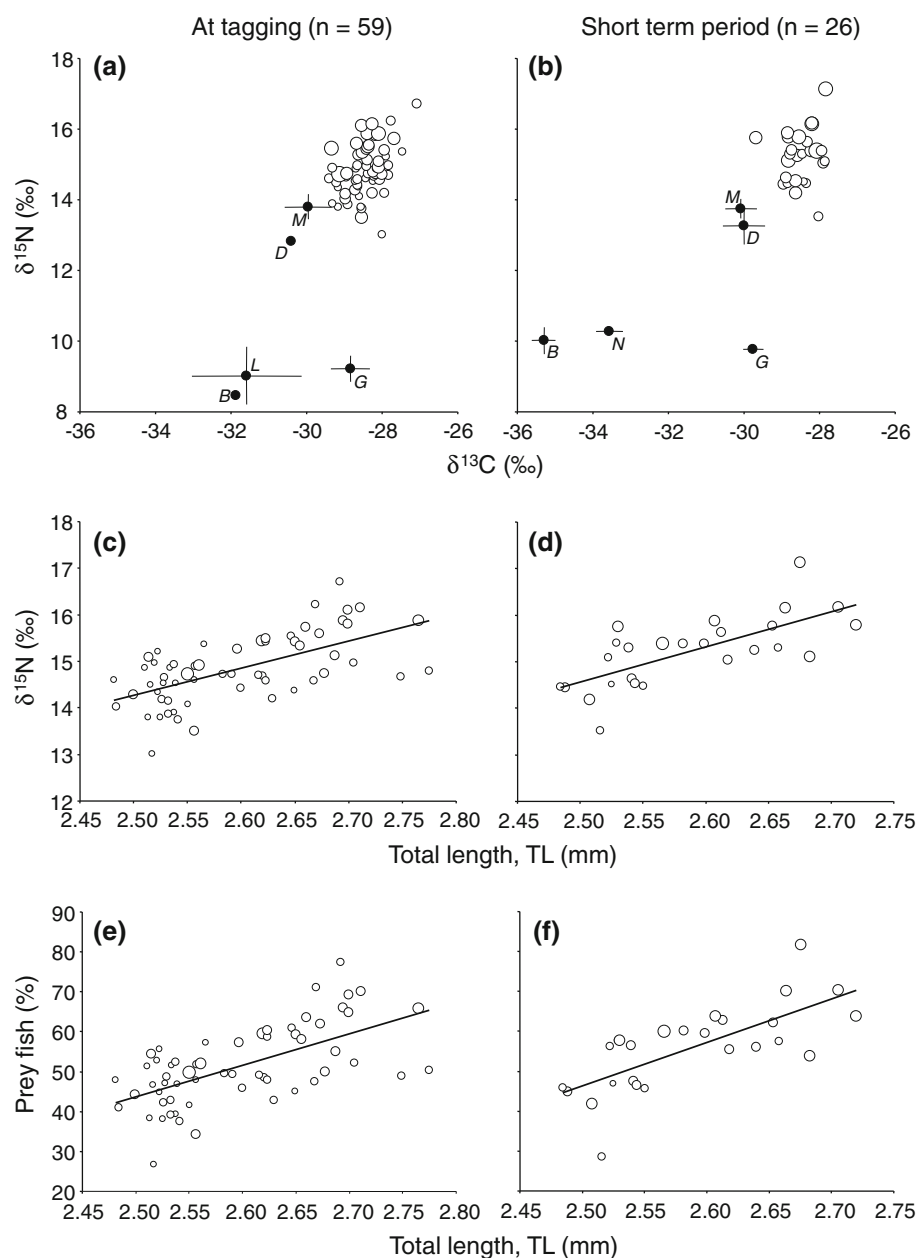
\* Significant at  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

<sup>a</sup> A model was built for each of the three trophic niche variables, i.e.  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ , and the contribution of prey fish to the diet (Prey Fish, obtained from the mixing models), respectively. Each model contained the HW:TL, TL (log-transformed) and the period [tagging period (June–July) and short-term period (August–October)] as predictors. Individual identity was used as a random factor

(Whiteley 2007). Thus, we highlight that individual specialisation in resource use and trophic morphology can occur at such small spatial scales with weaker niche segregation. However, care is needed on this latter point since integrating the entire diel variation in habitat use (Copp 2008) could have allowed detection of increased habitat niche segregation as eels are usually considered to be more active at night (Baras et al. 1998; Tesch 2003).

Eels with extreme trophic morphology (i.e. narrower and broader headed individuals) displayed higher body condition (i.e. fitness) than those with intermediate trophic morphology, which is in accordance with the prediction of a disruptive selection (e.g. Martin and Pfennig 2009). For example, Swanson et al. (2003) demonstrated experimentally that individual fitness was higher in polymorphic than in monomorphic cichlid (*Herichthys minckleyi*) populations, while Schluter (1995) observed that two forms of three-spine stickleback (*Gasterosteus aculeatus*) displayed higher fitness in their respective habitats (i.e. littoral zone and open water). Here, individuals with different trophic morphologies, coexisting in a small area with weak habitat segregation, displayed different fitness, as also observed by Martin and Pfennig (2009) with spadefoot toad tadpoles (*Spea multiplicata*). Furthermore, these authors demonstrated experimentally that these fitness differences could be explained by differences in foraging performances since individuals of intermediate trophic morphology fed less

**Fig. 3**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope values of eels (*white circles*) and their potential prey (*black circles*, mean  $\pm$  standard deviation) used in the mixing models during the tagging period (a) and during the short-term period (b). Prey items are minnow *Phoxinus phoxinus* (M), dace *Leuciscus leuciscus* (D), Brachycentridae (B), Limnephilidae (L), Gammaridae (G) and Neritidae (N). c, d Relationship between  $\delta^{15}\text{N}$  and TL of eels during the tagging period and the short-term period, respectively. e, f Contribution of prey fish to eel diet based on eel total length during the tagging period and the short-term period, respectively. The width of the *white circles* is proportional to the morphological index of each individual, i.e. broader headed individuals are represented by *wider circles*. Total length data is log transformed. Statistical details are provided in Table 2



efficiently in the alternative resources than individuals with extreme trophic morphology (Martin and Pfennig 2009). Given that prey fish are more energetically profitable than invertebrates but are more costly to capture and handle (e.g. Galarowicz and Wahl 2005), then it is likely that head morphology affects eel foraging performances where broader headed individuals forage more efficiently on fish as capture and handling times are reduced through increased mouth gape (e.g. Graeb et al. 2005). Narrower headed individuals might be then more efficient at detecting and capturing invertebrates. Since fitness was high for individuals with extreme trophic morphology, this suggests that differences in energy content of prey could be offset by optimising foraging performance on the alternative

resources. However, this remains speculative in the absence of experimental testing (e.g. Martin and Pfennig 2009).

Bulté et al. (2008) demonstrated that reproductive role contributes to sexual dimorphism in the trophic structure of Northern map turtles (*Graptemys geographica*), whereby females can increase their energy intake and fitness by ingesting larger prey. This raises the question about the potential interplay between sexual determination and individual specialisation in eel. Indeed, sex is environmentally determined in eel, and intraspecific competition, a factor cited as a cause for individual specialisation and disruptive selection (e.g. Smith and Skulason 1996; Bolnick et al. 2003; Bolnick 2004), is also implicated in sex

**Table 2** Results of the mixed linear models used to test for the effects of the morphological index on the habitat niche of European eels ( $n = 99$ )

Parameter <sup>a</sup>	Source of variation	df	Estimate (SE)	<i>p</i>
River width	TL	19	-0.002 (1.78)	0.999
	HW:TL	19	35.52 (58.74)	0.553
	Intercept	77	4.38 (9.75)	0.655
Substrate score	TL	19	-0.03 (0.45)	0.950
	HW:TL	19	-9.36 (14.86)	0.536
	Intercept	77	1.97 (2.47)	0.428
Vegetation cover	TL	19	-8.37 (10.20)	0.422
	HW:TL	19	218.35 (352.20)	0.543
	Intercept	77	71.80 (54.90)	0.195
Distance to the bank	TL	19	-1.54 (1.40)	0.283
	HW:TL	19	111.89 (46.28)	0.026*
	Intercept	77	6.15 (7.64)	0.423
Water velocity	TL	19	-0.02 (0.16)	0.895
	HW:TL	19	-4.75 (5.19)	0.372
	Intercept	77	0.60 (0.86)	0.488
Water depth	TL	19	28.86 (19.12)	0.148
	HW:TL	19	-475.81 (631.06)	0.460
	Intercept	77	-98.04 (104.82)	0.353

\* Significant at  $p < 0.05$

<sup>a</sup> A model was built for each of the six trophic niche variables (river width, substrate score, vegetation cover, distance to the bank, water velocity, and water depth). Each model contained the morphological index (HW:TL ratio) and TL (log-transformed) as predictors. Individual identity was used as a random factor

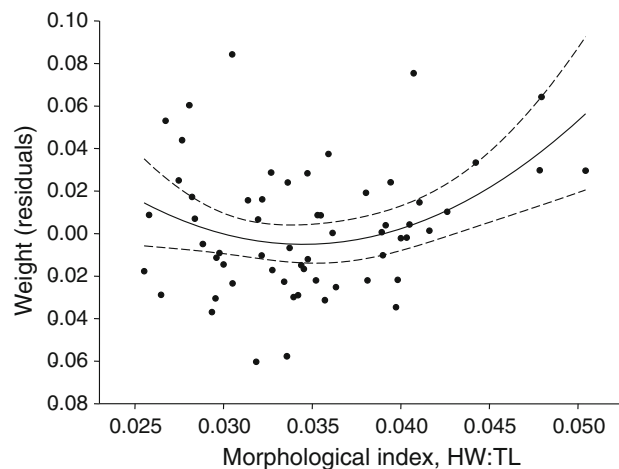
**Table 3** Results of the mixed linear model used to test for the effects of the morphological index on the body condition of European eels ( $n = 99$ )

Source of variation <sup>a</sup>	df	Standardised estimate (SE)	<i>p</i>
TL	36	0.54 (0.02)	<0.001***
Period: short term	36	-0.07 (0.02)	0.024*
Period: long term	36	-0.06 (0.02)	<0.001***
HW:TL	57	-0.36 (0.14)	0.013*
(HW:TL) <sup>2</sup>	57	0.37 (0.14)	0.009**
Intercept	57	4.73 (0.01)	<0.001***

<sup>a</sup> The model contained weight (W, log-transformed) as a response variable and the morphological index (HW:TL ratio), its quadratic term [(HW:TL)<sup>2</sup>], TL (log-transformed) and the period (tagging, short-term and long-term) as predictors. Individual identity was used as a random factor. The quadratic term allows for testing nonlinearity in the relationship between the morphological index and the body condition of eels. Standardised slope estimates are reported

\* Significant at  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$

determination (Davey and Jellyman 2005). Previous observations demonstrated that the proportion of males to females is higher in individuals with narrower heads, and

**Fig. 4** Relationship between residuals of eel weight (g) and the morphological index HW:TL (dashed lines  $\pm$  95% confidence intervals). Weight was log transformed in the mixed linear model. Each point represents the average residual value from the mixed linear model of each individually tagged eel ( $n = 60$ ) over the three periods. Statistical details are provided in Table 3

vice versa (Lammens and Visser 1989; Provan and Reynolds 2000). Altogether, these findings suggest a potential association between ecological specialisation, disruptive selection and sex differentiation that remains to be tested.

In conclusion, this study reveals substantial evidence for an association between individual specialisation and disruptive selection and provides a rare empirical example occurring at the fine spatial scale. Therefore, these results should stimulate further investigations on the role of resources heterogeneity and morphological variability on the shape of fitness function in wild populations. Given the crucial role of intraspecific competition and population density in driving the strength of disruptive selection and the fitness of individuals with variable morphological traits (Bolnick 2004), further investigations are needed to determine how competitive interactions can affect foraging performance and fitness and, subsequently, individual specialisation in wild populations.

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