



## Short communication

# Size-related variation in fecundity of European eel (*Anguilla anguilla*)

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Declining European eel (*Anguilla anguilla*) recruitment has focused attention on conservation of potential spawners leaving continental waters. Fecundity of wild, seaward-migrating silver-phase eels was shown to be size-related and higher than previously reported from artificial maturation experiments. Reliable information on fecundity is essential for stock modelling and future development of eel management policies.

**Keywords:** *Anguilla*, fecundity, female size, silver-phase eel, spawner stock management.

## Introduction

Since the 1980s, the European eel has undergone a serious population collapse throughout its range, and a variety of causes have been proposed (Stone, 2003). In response, the Council of the European Union (2007) has established a legislative framework (Council Regulation No. 1100/2007) to restore spawner escapement biomass from river basins to levels comparable (at least >40%) to those that occurred when pristine environmental conditions existed. Accordingly, European eel spawning dynamics have become a priority research area. Recent satellite tracking of the oceanic migration route (Aarestrup *et al.*, 2009) and swim trial experiments (e.g. Palstra and van den Thillart, 2010) have contributed to our understanding of the reproductive migration. The artificial completion of the Japanese eel *Anguilla japonica* life-cycle (Ijiri *et al.*, 2011) is encouraging for European researchers (PRO-EEL, 2011), although a complete understanding of the life-cycle and causes of the collapse of *A. anguilla* are necessary before artificial propagation will become a viable conservation action.

Current European eel stock recovery plans are almost entirely focused on increasing European eel escapement biomass. However, to determine what proportion of eels successfully migrate and reproduce, information on the health and quality status of potential spawners (e.g. Belpaire *et al.*, 2009; Clevestam *et al.*, 2011) is essential. In particular, knowledge of the

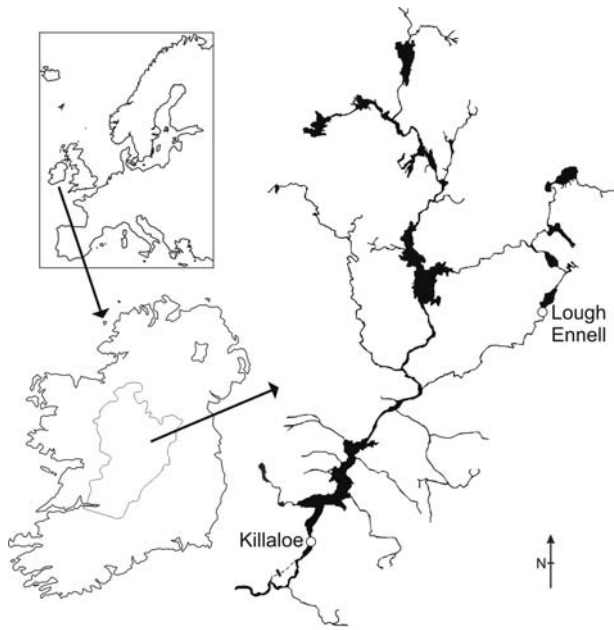
reproductive ecology, including fecundity, would enable estimation of the egg numbers required to maintain the standing stock, and could also facilitate future development of eel management policies.

A small number of published fecundity estimates of wild eels exist: for American eel *A. rostrata* (Wenner and Musick, 1974; Barbin and McCleave, 1997; Tremblay, 2009); New Zealand shortfin eel *A. australis*, and longfin eel *A. dieffenbachii* (Todd, 1981); *A. japonica* (Matsui, 1952); and the tropical giant mottled eel *A. marmorata* (Aoyama and Miller, 2003). It appears that European eel fecundity estimates are exclusively of artificially-matured eels (Kokhnenko *et al.*, 1977; Boetius and Boetius, 1980; van Ginneken *et al.*, 2005). Therefore, the aim of the present study was to estimate the fecundity of wild silver-phase European eels, captured undergoing their seaward spawning migration, and to relate this to body size.

## Material and methods

### Sampling area and collection

The Shannon International River Basin District, defined according to the Water Framework Directive (European Commission, 2010), occupies an area of 18 000 km<sup>2</sup>. The River Shannon predominantly drains the central lowlands of Ireland and discharges through a 97 km estuary into the North Atlantic (Figure 1). It is regulated



**Figure 1.** Silver eel sampling locations (Killaloe eel weir and Lough Ennell outlet) in the River Shannon catchment, Ireland.

for hydroelectric generation, and the mean annual discharge is  $186 \text{ m}^3 \text{ s}^{-1}$  (McCarthy and Cullen, 2000). During the 2007–2008 migration season, 25 silver-phase eels were randomly subsampled from the catch of a commercial fishing crew operating a winged stow net at the outlet of Lough Ennell ( $53^{\circ}27'N$   $7^{\circ}23'W$ ). This  $14.3 \text{ km}^2$  mesotrophic lowland lake in the upper Shannon catchment forms part of the River Brosna tributary. The limited size range of Lough Ennell eels (84% were 630–750 mm) precluded analysis of the complete River Shannon female size range (McCarthy and Cullen, 2000) from this location. Therefore, during the 2008–2009 migration season, supplementary silver-phase eels were obtained at Killaloe eel weir ( $52^{\circ}48'N$   $8^{\circ}27'W$ ) on the lower River Shannon. Thirteen eels were selected from the catch, to represent the entire River Shannon female size range. The fishing gears at both locations captured all sizes of female silver-phase eels (McCarthy and Cullen, 2000; Tesch, 2003).

### Treatment and analysis

Eels were sacrificed by immersion in a solution of clove oil and ethanol in water. The body length (to the nearest 1 mm) and body weight ( $\pm 1 \text{ g}$ ) of each eel was recorded. Horizontal and vertical eye diameters were measured to the nearest 0.1 mm for Killaloe eels only, and eye index was calculated as:

$$\left\{ \left[ \frac{(\text{horizontal eye diameter} + \text{vertical eye diameter})}{4} \right]^2 \times \pi / \text{total length} \right\} \times 100$$

(Pankhurst, 1982). Sex was determined by macroscopic examination of the gonads (Tesch, 2003) and all eels were confirmed to be females. Both ovaries were removed from the body cavity and weighed to the nearest 0.01 g. Gonadosomatic index (GSI) was calculated as:

$$(\text{gonad weight} / \text{body weight}) \times 100$$

(Durif *et al.*, 2005). Eels were classified as silver-phase by external appearance, eye index  $> 6.5$  (Pankhurst, 1982; Aoyama and Miller, 2003) (Killaloe eels only) and  $\text{GSI} > 1.2\%$  (Durif *et al.*, 2005) (all eels). Treatment with 250 ml 2% acetic acid was carried out on fresh ovaries following the protocol described by Barbin and McCleave (1997). Each solution was agitated daily, and all eggs/ovarian tissue were separated within 7 days. The solutions were then diluted using distilled water. Most (76.3%) eels were diluted to 2 l, but the larger eels were diluted to 6–10 l (Barbin and McCleave, 1997). Egg counts were made on 1 ml volumetric subsamples examined at  $\times 40$  magnification. Four subsamples were counted and an estimate of fecundity was calculated by reference to the mean egg count and the dilution factor (Barbin and McCleave, 1997; Tremblay, 2009). Body length, body weight, gonad weight, and number of eggs (fecundity) were  $\log_{10}$ -transformed to meet the requirements of parametric analysis (i.e. normality and equality of variances). Pearson correlation coefficients ( $r$ ) were calculated for the relationships between fecundity–length, fecundity–body weight and fecundity–gonad weight. Simple linear regression analysis of length on body weight and fecundity on length were undertaken following the form:

$$\log Y = a + b \log X$$

Differences between the intercept and slope of the Killaloe and Lough Ennell fecundity–length regression equations were tested using the General Linear Test Method (Neter *et al.*, 1996).

### Results

A within-river comparison of the fecundity–size relationship showed no difference between sampling location [General Linear Test:  $F = 0.313$ ;  $d.f.$  (degrees of freedom) = 2, 34;  $p = 0.73$ ]. Therefore, all data were pooled and analysed as a single River Shannon sample ( $n = 38$ ). The length–body weight relationship is given by the equation:

$$\log_{10} \text{ length} = 1.991 (\pm 0.033) + 0.302 (\pm 0.012) \\ \times \log_{10} \text{ body weight} (r^2 = 0.949, p < 0.001)$$

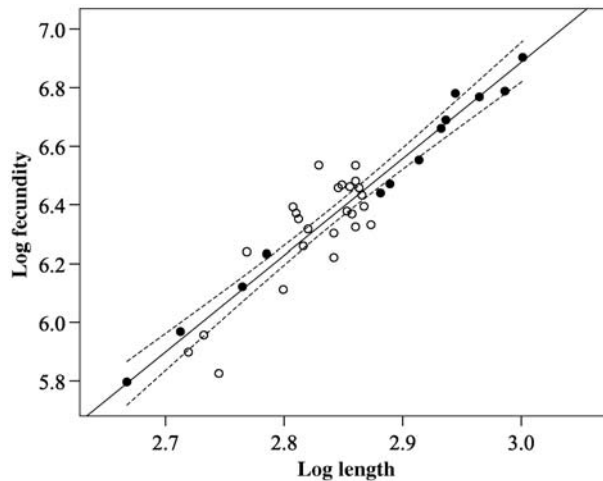
Values in parentheses are standard error of mean (S.E.M.). Fecundity was positively correlated with length ( $r = 0.943$ ;  $p < 0.001$ ), body weight ( $r = 0.955$ ;  $p < 0.001$ ) and gonad weight ( $r = 0.936$ ;  $p < 0.001$ ), and increased exponentially with length according to the following regression equation:

$$\log_{10} \text{ fecundity} = -2.992 (\pm 0.550) + 3.293 (\pm 0.193) \\ \times \log_{10} \text{ length} (r^2 = 0.889; p < 0.001)$$

The  $\log_{10}$ -transformed fecundity–length regression (and associated 95% confidence intervals) is illustrated (Figure 2). Fecundity estimates for the eels examined ranged from 626 000 to 8 006 667 for individuals of 465 mm (211 g) to 1003 mm (2472 g). Based on the fecundity–length regression equation, these eels would have estimated fecundities of 619 331 to 7 785 455. The relative fecundity (eggs/kg) was estimated to be 3 591 699. The morphological characteristics and fecundity of the silver-phase eels examined (by location and pooled data) are presented in Table 1.

## Discussion

Fecundity in the temperate eels *A. rostrata* (Wenner and Musick, 1974; Barbin and McCleave, 1997; Tremblay, 2009), *A. australis* and *A. dieffenbachii* (Todd, 1981) has been shown to increase exponentially with increasing body size (Table 2). In the present study, which provides the first fecundity estimates of wild *A. anguilla*, fecundity was also shown to be size-related in this species. No difference in fecundity–size relationship was observed between the upper and lower River Shannon sampling locations. Tremblay (2009) did find differences in fecundity between five subpopulations of *A. rostrata* in a large North American catchment



**Figure 2.** Log<sub>10</sub>-transformed fecundity–length regression of pooled River Shannon (Killaloe; closed circles, Lough Ennell; open circles) silver-phase eels, with 95% confidence intervals.

(Saint Lawrence River), but concluded that this was not related to migration distance. However, considerable variation in *A. rostrata* fecundity estimates from Chesapeake (37°N) (Wenner and Musick, 1974), Maine (45°N) (Barbin and McCleave, 1997) and the Saint Lawrence (44–49°N) (Tremblay, 2009) suggest differences may exist on a larger spatial (or temporal) scale (Table 2). No such data is available for *A. anguilla* at present, but possible geographical variation in reproductive potential, reflecting energy requirements and migration distance, has been suggested by Belpaire *et al.* (2009).

Factors other than spatial variation may also affect fecundity. The accumulation of lipophilic compounds in gonads may reduce egg production and development (e.g. Belpaire *et al.*, 2009). The water quality of the River Shannon is mainly classified as unpolluted (Lucey, 2009) and in general, contaminant levels in Irish eels are low compared to other European countries (McHugh *et al.*, 2010). Habitat use and migratory type may also affect fecundity, as observed in relation to other biological characteristics (e.g. Svedäng *et al.*, 1996; Arai *et al.*, 2006). Otolith microchemical analysis of upper and lower River Shannon eels indicates that the eel populations are composed almost entirely of freshwater residents (Arai *et al.*, 2006). It seems that further eel fecundity studies from a range of locations may be necessary, particularly when significant differences in biological characteristics can occur even at the scale of neighbouring catchments (Acou *et al.*, 2009). Furthermore, silver-phase eel quality and maturation status within a river system may also change during the downstream migration season, and this should be incorporated in a more comprehensive sampling programme.

Differences between wild and artificially-matured *A. anguilla* fecundity estimates (Table 2) may be due to the methodology used, or may reflect changes in the gonads accompanying the

**Table 1.** Summary of the morphological characteristics and fecundity of the silver-phase eels examined.

	L. Ennell (n = 25)			Killaloe (n = 13)			Pooled (n = 38)		
	Mean	± S.E.	Min–max	Mean	± S.E.	Min–max	Mean	± S.E.	Min–max
Length (mm)	673	13	524–747	771	49	465–1003	707	20	465–1003
Weight (g)	587	31	267–798	1121	188	211–2472	770	78	211–2472
GSI (%)	1.75	0.06	1.24–2.57	1.66	0.05	1.44–1.99	1.72	0.04	1.24–2.57
Eye index				7.13	0.30	6.54–10.57			
Fecundity (millions)	2.23	0.15	0.67–3.43	3.80	0.65	0.63–8.01	2.76	0.27	0.63–8.01

**Table 2.** Summary of anguillid fecundity studies.

Species	Study	Size range	Min–max fecundity (millions of eggs)	Relative fecundity (millions of eggs/kg)
<i>A. anguilla</i>	Kokhnenko <i>et al.</i> (1977) <sup>§</sup>	N/a	N/a	3.0
	Boetius and Boetius (1980) <sup>§</sup>	640–920 mm	0.7–2.6	1.6
	van Ginneken <i>et al.</i> (2005) <sup>§</sup>	690–870 mm	0.8–4.0	1.8
	This study	465–1003 mm	0.6–8.0	3.6
<i>A. rostrata</i>	Wenner and Musick (1974)	490–724 mm	0.5–2.6	3.8 <sup>†</sup>
	Barbin and McCleave (1997)	452–1133 mm	1.7–20.7	8.1 <sup>†</sup>
	Tremblay (2009)	532–1159 mm	3.4–22.0	6.5–10.0
<i>A. australis</i>	Todd (1981)	516–933 mm	0.5–3.1	1.9
<i>A. dieffenbachii</i>	Todd (1981)	711–1452 mm	1.1–20.8	2.0
<i>A. japonica</i>	Matsui (1952)	357–924 mm	7.2–12.7	N/a
<i>A. marmorata</i>	Aoyama and Miller (2003)	2400 g	34.8	N/a

<sup>§</sup>Eels were artificially-matured.

<sup>†</sup>Estimated from the regression equation for a 1 kg eel.

maturation process. The treatment of ovaries with 2% acetic acid and subsequent volumetric subsampling has successfully been used in previous anguillid fecundity studies (Barbin and McCleave, 1997; Tremblay, 2009). However, *A. anguilla* fecundity estimates obtained by Boetius and Boetius (1980) by counting eggs retained by a 0.224 mm mesh, were underestimated, as only eggs which had responded to hormonal treatment were counted, and the relative fecundity (eggs/kg) reported (1.6 million) is less than half that obtained in the present study (3.6 million). Likewise, the relative fecundity of artificially-matured *A. anguilla* by van Ginneken *et al.* (2005) is considerably lower (1.8 million) than in the present study, possibly reflecting the counting method (gravimetric subsampling) or an effect of the artificial maturation process. Russian maturation experiments conducted in the 1970s quote a relative fecundity of 3 million (Kokhnenko *et al.*, 1977), although no details of counting method are described.

The application of fecundity estimates derived from artificial maturation experiments to wild eel populations may not be appropriate, given the issues discussed above. Similarly, fecundity estimates derived from wild eels captured in continental waters (i.e. early vitellogenic stage) may differ from the actual fecundity at the spawning grounds. Ideally, eels in advanced spawning condition (mid-/late-vitellogenic stage) should be examined. However, to date only female eels of *A. japonica* and *A. marmorata* have been captured at their spawning grounds (Ijiri *et al.*, 2011). Analysis of changes in the number of eggs in the gonads during the maturation process may be possible using artificially-matured eels (e.g. Durif *et al.*, 2006), although the extent to which hormonal treatment reflects the natural maturation of eels at sea will need to be verified. The limited reproductive success of artificial maturation experiments with *A. anguilla* (Pedersen, 2004; Palstra *et al.*, 2005) suggests that hormonal treatment results in certain artifactual outcomes (e.g. poor egg quality, delayed hatching and abnormal morphology), which may bias fecundity estimates.

Different growth strategies have been proposed for female eels during the continental phase of the lifecycle i.e. size-maximizing, with its associated higher pre-reproductive mortality rates, to achieve maximum fecundity (e.g. Davey and Jellyman, 2005) or time-minimizing (Svedäng *et al.*, 1996). Laboratory observations of the spawning behaviour of artificially-matured eels suggest batch spawning by females (Boetius and Boetius, 1980), and that a single male may be capable of fertilizing several egg batches (van Ginneken *et al.*, 2005). If this is typical of natural spawning events, female eels could be considered of greater reproductive value than males. Therefore, stock recovery plans should prioritize the protection of large, highly fecund, female eels. Clevestam *et al.* (2011) proposed similar protection measures for large females in the Baltic Sea, as their large size and high lipid content would make them most likely to successfully migrate and spawn (Belpaire *et al.* 2009; Palstra and van den Thillart, 2010).

Modelling of *A. anguilla* population dynamics has been attempted using fisheries data (Dekker, 2000), demographics (van der Meer *et al.*, 2011), and integrated genetic and demographic models (Pujolar *et al.*, 2010; Andrello *et al.*, 2011). Such models often involve numerous input variables, including fecundity. However, the use of differing fecundity estimates [e.g. Boetius and Boetius (1980) in Andrello *et al.* (2011); Barbin and McCleave (1997) in Pujolar *et al.* (2010)] has a knock-on effect on subsequent calculations, and it would seem that neither estimate is appropriate, as respectively, they relate to artificially-matured eels (underestimate) and *A. rostrata* (overestimate) (see Table 2).

Van der Meer *et al.* (2011) reject both of these estimates and instead use a notional figure of 2 million eggs for a 560 g eel, which is very similar to our presented data (1.98 million).

Andrello *et al.* (2011) divided the continental eel stock into three production units (North, north of 50°N; Atlantic, between 35°N and 50°N; Mediterranean, south of 35°N), with a sex ratio of 0.34 females in the breeding stock and mean female silver-phase eel sizes of 663 mm, 664 mm and 572 mm in each unit respectively. Applying this scenario to Dekker's (2000) estimate of silver-phase eel escapement (8.8 million), we calculate an *A. anguilla* population fecundity of  $5.21 \times 10^{12}$  million eggs based on the mean size of eels in each production unit, and the fecundity-length relationship presented in Figure 2

The currently available models do not take into account the complexities associated with, for example, the impact of pollution on gonadal development and egg production (e.g. Belpaire *et al.*, 2009), or the possibility of multiple spawning events (Boetius and Boetius, 1980; Ijiri *et al.*, 2011). However, as illustrated by the present study, the need for reliable knowledge of eel fecundity and other population parameters is important for population modelling and spawner stock management. Integration of data on various aspects of European eel biology (fecundity, mating dynamics, larval survival, recruitment, escapement, spawning migration, demographics etc.) may enable estimation of total spawner numbers required in the Sargasso Sea to maintain the standing stock. If possible, this would represent a major step in the conservation of this endangered species.

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## References

- Aarestrup, K., Økland, F., Hansen, M. M., Righton, D., Gargan, P., Castonguay, M., Bernatchez, L., *et al.* 2009. Oceanic spawning migration of the European eel (*Anguilla anguilla*). *Science*, 325: 1660.
- Acou, A., Gaele, G., Feunteun, E., and Laffaille, P. 2009. Differential production and condition indices of premigrant eels in two small Atlantic coastal catchments of France. *In* Eels at the Edge: Science, Status and Conservation Concerns, pp. 157–174. Ed. by J. Casselman, and D. K. Cairns. American Fisheries Society Symposium 58. 460 pp.
- Andrello, M., Bevacqua, D., Maes, G. E., and De Leo, G. A. 2011. An integrated genetic-demographic model to unravel the origin of genetic structure in European eel (*Anguilla anguilla* L.). *Evolutionary Applications*, 4: 517–533.
- Aoyama, J., and Miller, M. J. 2003. The silver eel. *In* Eel Biology, pp. 107–117. Ed. by K. Aida, K. Tsukamoto, and K. Yamauchi. Springer, Tokyo. 497 pp.
- Arai, T., Kotake, A., and McCarthy, T. K. 2006. Habitat use by the European eel *Anguilla anguilla* in Irish waters. *Estuarine, Coastal and Shelf Science*, 67: 569–578.
- Barbin, G. P., and McCleave, J. D. 1997. Fecundity of the American eel *Anguilla rostrata* at 45°N in Maine, U.S.A. *Journal of Fish Biology*, 51: 840–847.
- Belpaire, C. G. J., Goemans, G., Geeraerts, C., Quataert, P., Parmentier, K., Hagel, P., and De Boer, J. 2009. Decreasing eel stocks: survival of the fattest? *Ecology of Freshwater Fish*, 18: 197–214.
- Boetius, I., and Boetius, J. 1980. Experimental maturation of female silver eels, *Anguilla anguilla*. Estimates of fecundity and energy reserves for migration and spawning. *Dana*, 1: 1–28.



- Clevesam, P. D., Ogonowski, M., Sjöberg, N. B., and Wickström, H. 2011. Too short to spawn? Implications of small body size and swimming distance on successful migration and maturation of the European eel *Anguilla anguilla*. *Journal of Fish Biology*, 78: 1073–1089.
- Council of the European Union. 2007. Council regulation (EC) No 1100/2007 of 18 September 2007 establishing measures for the recovery of the stock of European eel. *Official Journal of the European Union*, 248: 17–23.
- Davey, A. J., and Jellyman, D. J. 2005. Sex determination in freshwater eels and management options for manipulation of sex. *Reviews in Fish Biology and Fisheries*, 15: 37–52.
- Dekker, W. 2000. A Procrustean assessment of the European eel stock. *ICES Journal of Marine Science*, 57: 938–947.
- Durif, C., Dufour, S., and Elie, P. 2005. The silvering process of *Anguilla anguilla*: A new classification from the yellow resident to the silver migrating stage. *Journal of Fish Biology*, 66: 1025–1043.
- Durif, C., Dufour, S., and Elie, P. 2006. Impact of silvering stage, age, body size and condition on reproductive potential of European eel. *Marine Ecology Progress Series*, 327: 171–181.
- European Commission. 2010. The Water Framework Directive (2000/60/EC). Directorate-General for the Environment, [http://ec.europa.eu/environment/water/water-framework/index\\_en.html](http://ec.europa.eu/environment/water/water-framework/index_en.html) (last accessed 5 October 2011).
- Ijiri, S., Tsukamoto, K., Chow, S., Kurogi, H., Adachi, S., and Tanaka, H. 2011. Controlled reproduction in the Japanese eel (*Anguilla japonica*), past and present. *Aquaculture Europe*, 36: 13–17.
- Kokhnenko, S. V., Bezdenezhnykh, V. A., and Gorovaya, S. L. 1977. Maturation of the European eel, *Anguilla anguilla*, when artificially reared. *Journal of Ichthyology*, 17: 878–883.
- Lucey, J. 2009. Water Quality in Ireland 2007–2008: Key Indicators of the Aquatic Environment. Environmental Protection Agency, Ireland. 44 pp.
- Matsui, I. 1952. Studies on the morphology, ecology and pond culture of the Japanese eel (*Anguilla japonica* Temminck and Schlegel). *Journal of the Shimonoseki College of Fisheries*, 2: 1–245.
- McCarthy, T. K., and Cullen, P. 2000. The River Shannon silver eel fisheries: variations in commercial and experimental catch levels. *Dana*, 2: 59–68.
- McHugh, B., Poole, R., Corcoran, J., Anninou, P., Boyle, B., Joyce, E., Foley, M. B., *et al.* 2010. The occurrence of persistent chlorinated and brominated organic contaminants in the European eel (*Anguilla anguilla*) in Irish waters. *Chemosphere*, 79: 305–313.
- Neter, J., Kutner, M. H., Wasserman, C., and Nachtsheim, C. 1996. *Applied Linear Statistical Models*, 4th edn. McGraw-Hill, Columbus. 1408 pp.
- Palstra, A. P., Cohen, E. G. H., Niemantsverdriet, P. R. W., van Ginneken, V. J. T., and van den Thillart, G. E. E. J. M. 2005. Artificial maturation and reproduction of European silver eel: development of oocytes during final maturation. *Aquaculture*, 249: 533–547.
- Palstra, A. P., and van den Thillart, G. E. E. J. M. 2010. Swimming physiology of European silver eels (*Anguilla anguilla* L.): energetic costs and effects on sexual maturation and reproduction. *Fish Physiology and Biochemistry*, 36: 297–322.
- Pankhurst, N. W. 1982. Relation of visual changes to the onset of sexual maturation in the European eel *Anguilla anguilla* (L.). *Journal of Fish Biology*, 21: 127–140.
- Pedersen, B. H. 2004. Fertilisation of eggs, rate of embryonic development and hatching following induced maturation of European eel *Anguilla anguilla*. *Aquaculture*, 237: 461–473.
- PRO-EEL, 2011. Reproduction of European Eel towards a self-sustained aquaculture. <http://www.pro-eel.eu/> (last accessed 2 July 2012).
- Pujolar, J. M., Bevacqua, D., Andreello, M., Capoccioni, F., Ciccotti, E., De Leo, G. A., and Zane, L. 2010. Genetic patchiness in European eel adults evidenced by molecular genetics and population dynamics modelling. *Molecular Phylogenetics and Evolution*, 58: 198–206.
- Stone, R. 2003. Freshwater eels are slip-sliding away. *Science*, 302: 221–222.
- Svedäng, H., Neuman, E., and Wickström, H. 1996. Maturation patterns in female European eel: age and size at the silver eel stage. *Journal of Fish Biology*, 48: 342–351.
- Tesch, F. W. 2003. *The Eel*, 3rd edn. Blackwell Science, Oxford. 408 pp.
- Todd, P. R. 1981. Morphometric changes, gonad histology, and fecundity estimates in migrating New Zealand freshwater eels (*Anguilla* spp.). *New Zealand Journal of Marine and Freshwater Research*, 15: 155–170.
- Tremblay, V. 2009. Reproductive strategy of female American eels among five subpopulations in the St. Lawrence River watershed. In *Eels at the Edge: Science, Status and Conservation Concerns*, pp. 85–102. Ed. by J. Casselman, and D. K. Cairns. American Fisheries Society Symposium 58. 460 pp.
- van der Meer, J., van der Veer, H. W., and Witte, J. I. J. 2011. The disappearance of the European eel from the western Wadden Sea. *Journal of Sea Research*, 66: 434–439.
- van Ginneken, V., Vianen, G., Muusze, B., Palstra, A., Verschoor, L., Lugten, O., Onderwater, M., *et al.* 2005. Gonad development and spawning behaviour of artificially-matured European eel (*Anguilla anguilla* L.). *Animal Biology*, 55: 203–218.
- Wenner, C. A., and Musick, J. A. 1974. Fecundity and gonad observations of American eel, *Anguilla rostrata*, migrating from Chesapeake Bay, Virginia. *Journal of the Fisheries Research Board of Canada*, 31: 1387–1391.

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