



The role of a freshwater tidal area with controlled reduced tide as feeding habitat for European eel (*Anguilla anguilla*, L.)

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Summary

Implementation of the Controlled Reduced Tide (CRT) technique could increase the total surface of tidal freshwater marshes in Europe and ease implementation of restoration projects in coastal defense and riverine ecosystems. The goal was to determine whether a regularly flooded area connected to a freshwater tidal river could act as an important foraging area for European eel, and if so, to what extent the diet of eels in this flooding area differed from that of eels foraging in the river itself. The stomach contents of eels from the River Schelde were compared with eels from the Lippenbroek, an adjacent CRT area. Prey diversity (H') of individual eels was about four times higher in the Lippenbroek than in the River Schelde. Moreover, 12 prey categories in eel stomachs from the Lippenbroek were found whereas only three categories were retrieved from eels in the River Schelde. In the Lippenbroek, eels fed on terrestrial organisms (lumbricids, caterpillars and other insects), but also on fish and fish eggs and to a lesser extent on other aquatic prey (Lumbricullidae, chironomids and Hirudinea). In contrast, eels from the main river fed mainly on tubificids, fish, and some gammarids. Consequently, eels in the Schelde estuary are opportunistic feeders, but with a preference for large benthic prey. The number and weight of aquatic organisms ingested by eels in the Lippenbroek is not significantly different from the River Schelde. However, eels foraging in the Lippenbroek area had consumed significantly more terrestrial prey. Furthermore the total caloric value estimated for the ingested prey of eels from the Lippenbroek (derived from the literature) was about twice as high as that for eels from the River Schelde. While the condition index remained inconclusive, an Ancova revealed that eels captured in the Lippenbroek were significantly heavier for a given length than eels captured in the Schelde. The study showed that with a controlled reduced tide to restore lateral connectivity of large tidal rivers with their adjacent floodplains, high quality habitats for the European eel are created. These measures could significantly contribute to the production of eels in better condition, which have better chances to reproduce successfully. Hence, wetland restoration could enhance the recovery of the European eel stocks.

Introduction

During the past century, human activities have reduced the intertidal areas of many river systems throughout the world.

As a result of dike construction and land reclamation for agricultural, urban, industrial or port development, tidal areas have been reduced dramatically. Many estuaries, including the Schelde estuary, suffer from degradation and a loss of habitat because the intertidal zone shifted from a natural state towards a river system, with little or no lateral connectivity with their former floodplains (Maris et al., 2007). However, intertidal areas in estuaries play a multifunctional role, from energy dissipation and mitigation of floods over sedimentation and aeration (Cox et al., 2006; Maris et al., 2007) to a contribution to the nutrient cycle (Gribsholt et al., 2005; Struyf et al., 2005). It is believed that the natural development can be enhanced by combining the concept of a flood control area with the functions of intertidal areas. To this end, and in the framework of natural development, these habitats are currently being rehabilitated or even recreated (e.g. by creating inundation areas with a controlled reduced tide; see Methods for further details) (Meire et al., 2005; Cox et al., 2006; Maris et al., 2007).

However, the importance for fishes of these tidal marshes, especially those located in the oligohaline and freshwater tidal zone of an estuary is not yet entirely clear, in contrast to salt marsh creeks and intertidal marine areas (cf. Cattrijsse and Hampel, 2006). Some authors describe freshwater natural inundation areas as spawning grounds and nursery habitats for many organisms including fishes. Rozas and Odum (1987a) and Hohausová et al. (2003), for instance, observed fish spawning movements between the rivers and their backwaters or flooding areas. Rozas and Odum (1987b) and Breine et al. (2009) emphasise the importance of creeks in tidal marshes as habitats for juvenile fishes. The high number of juveniles caught in tidal freshwater marshes suggests that they could serve as an important nursery habitat. Despite this extensive knowledge on the nursery habitat function of fresh water tidal marshes, less is known about their specific function as feeding grounds for freshwater fishes. However, Rozas and Odum (1987a) suggest that plant beds in tidal freshwater creeks might be important foraging habitats, while T. Maris and O. Beauchard (personal comment) regularly observed foraging behaviour of fishes in vegetation zones during high tide. Moreover, Lasne et al. (2008) revealed that in downstream river segments the eels were in poorer condition in disconnected waterbodies than in connected ones, suggesting the importance of intertidal marshes. However, few quantitative data exist that actually demonstrate the

use of freshwater estuarine inundation areas as foraging habitat by fishes, as for instance the European eel (*Anguilla anguilla*, L.).

The European eel is currently listed as 'critically endangered' on the IUCN Red List of threatened species (Freyhof and Brooks, 2011). The abundance of the European glass eel decreased significantly within the last decades by 90–98% (Dekker et al., 2003; Bark et al., 2007). All European elver recruitment-series demonstrate clear and marked decadal reductions since the early 1980s. For the last 5 years the elver-based series averaged between 1% (continental North Sea) and < 5% elsewhere in Europe compared to the mean for 1960–1979 levels (Gollock et al., 2011; WGEEL, 2011). Overall recruitment since records began remains at an all time low, and the stock continues to decline. Currently, there are indications that the eel stock is at an historical minimum and is outside safe biological limits (WGEEL, 2010, 2011). This has drawn the attention of the European Union, which elaborated a framework with eel management measures for restoration of the eel stock since 2007, currently being implemented by the EU member-states through national eel management plans (EC, 2007). For a better implementation, more information and research on the biology of eel is needed. Many aspects of eel biology are still insufficiently understood (Tesch, 2003; Dekker, 2004; Van Ginneken and Maes, 2006), such as habitat use and the feeding ecology of yellow eels. Mathieson et al. (2000) found extremely high abundances of eel in freshwater tidal marshes, sometimes even dominating the local fish assemblage; however, little is known about the use of both natural and regulated tidal areas as potential foraging habitats (Lafaille et al., 2004). If tidal areas provide optimal foraging environments for eel, the creation of these habitats might contribute significantly to eel stock restoration by producing high quality eels that are able to reach their spawning grounds to spawn successfully.

Whereas the effect of prey intake on the condition of eels is poorly understood, food preferences of eel have been described previously (Bergersen and Klemetsen, 1988; Yalçın-Özdilek and Solak, 2007; Bouchereau et al., 2009a; Dörner et al., 2009). Bouchereau et al. (2009a) found that eels tend to consume benthic prey that are most abundant at a particular time. In general, eels appear to be bottom-dwelling predators feeding mainly on epibenthic and periphytic invertebrates and small fishes (Bergersen and Klemetsen, 1988; Belpaire et al., 1992; Dörner et al., 2009). Dörner et al. (2009) even showed that piscivory by eels appeared negligible when macro-invertebrate (insects) availability was high. Moreover, eels can switch easily between benthic and pelagic food webs, but prefer benthic prey if available, even at high densities of potential prey fish (Dörner et al., 2009). The European eel thus seems to adapt its diet to the available resources offered by the ecosystem (Bergersen and Klemetsen, 1988; Yalçın-Özdilek and Solak, 2007; Bouchereau et al., 2009a,b; Dörner et al., 2009), suggesting an opportunistic feeding strategy in European eel but with a preference for macro-invertebrate prey.

This study focuses on habitat use and feeding habits of yellow eels in a recently created inundation area with a controlled reduced tide along the River Schelde in Belgium. We hypothesise that in a regulated tidal freshwater inundation area the presence of higher prey diversity and different caloric values of prey will be of advantage to eels using inundated areas as foraging habitats, compared to individuals feeding in the main river. This could result in fatter eels, which likely have a higher probability of successful reproduction.

Four specific research questions were posed: (i) do eels use a CRT area as foraging habitat and, if so, (ii) does the food composition differ between a CRT area and an adjacent river site, (iii) does the caloric content of individual stomach contents differ among sites and (iv) do condition factors or length-weight relationships of eels differ among sites.

Materials and methods

Study area

An extensive description of the study site is given in Maris et al. (2008) and Beauchard et al. (2011). The Lippenbroek is an area of controlled reduced tidal movements of 8 ha connected to the River Schelde, Belgium (Fig. 1; 51°06'17"N; 4°08'00"E). After installing the tidal regime in March 2006 with a sluice construction, water from the Schelde River now enters the Lippenbroek during flooding and leaves during ebb tide, thus mimicking the natural dynamics of mudflats and tidal marshes but with a reduced tidal regime. Almost no water enters at neap tide, but the entire Lippenbroek floods during spring tide. The tidal amplitude is reduced, on average, from 5.5 m in the Schelde to 1.3 m in the pilot CRT and the high water level is about 3 m lower in the polder than in the Schelde. The spring neap tidal cycle is, however, maintained (Maris et al., 2008; Beauchard et al., 2011). Mean depth at low tide is 0.5 m in the main creek and approximately 1 m at the inlet reservoir. In the northern part of the Lippenbroek area there is a second permanent but shallow waterbody with a mean depth at low tide of 0.2 m (Fig. 1).

The CRT technique is very new and implemented for the first time in Belgium. The Lippenbroek is a pilot site showing that tidal marsh restoration is possible on embanked sites with elevations below the level of mean high water. The novel CRT technique can be of interest for many estuaries since it allows tidal marsh restoration on sites that are not suitable for managed realignment. This pilot project aimed to evaluate the ecological effects of a flood control area (Meire et al., 2005; Maris et al., 2007). An extensive program of tidal characteristics, natural development, and water quality was monitored

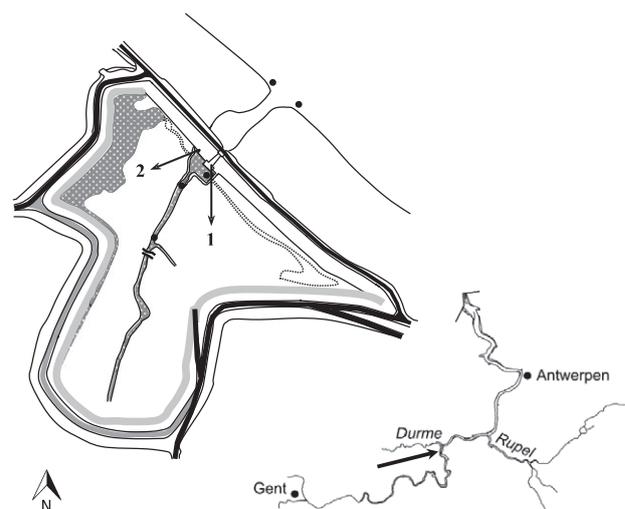


Fig. 1. The Lippenbroek, a freshwater tidal marsh with a Controlled Reduced Tide (CRT) along the Schelde estuary, located upstream of the Durme mouth. Fyke net positions (●) and permanent water bodies in the Lippenbroek area are shown (■). Arrows 1 and 2 = location of inlet and outlet (adapted from Simoens et al., 2007)

for the Lippenbroek area from March 2006 to March 2010 (Beauchard et al., 2011). Typical tidal freshwater vegetation has developed after 2 years of a daily controlled, reduced tide. Jacobs et al. (2009) showed that the arrival and establishment of typical tidal freshwater marsh vegetation was rapid, and caused by the eradication of terrestrial plant species and colonisation by estuarine vegetation in the Lippenbroek.

Maris et al. (2008) presented the first results on species colonisation and habitat development in the Lippenbroek. Benthic prey availability in the study area is quantified by the study of Beauchard et al. (submitted). After 1 year species richness of macro-invertebrates in the frequently flooded sites already exceeded that observed in the river sites, while some taxa absent in the river were observed in the Lippenbroek area and oligochaete densities exceeded the river site densities six-fold. After 3 years, macro-invertebrate colonisation continued, albeit at a lower pace, on the less frequently flooded sites. Not surprisingly, this tidal marsh is also inhabited by terrestrial species. Beauchard et al. (submitted) found annelids (Lumbricidae and Enchytraeidae), Chilopoda, Diplopoda, Collembola, terrestrial isopods and five different taxa of terrestrial coleoptera: *Carabidae*, *Chrysomelidae*, *Curculionidae*, *Elateridae* and *Staphylinidae* in the freshwater tidal marsh of the Lippenbroek.

Sampling

Yellow eels were captured simultaneously in the Lippenbroek and the River Schelde using fyke nets in the subtidal zone (Fig. 1). The nets were emptied at dawn after 24 h (at low tide). Samples of live eels were collected in April (25/04/2006) and May (23/05/2006). Total length (TL) was measured to the nearest 0.1 cm and body mass (BM) measured to the nearest 0.1 g (Sartorius Balance BL6100). Only eels landed with the fyke nets < 2 h before handling were used for food analyses in order (1) differences in stomach content caused by specific digestion rates of prey and (2) an overestimation of empty stomachs. All eels used for food analyses were killed by an overdose of anaesthetic (MS222). Stomachs and guts were removed *in situ*, labelled and fixed in 10% formalin.

Stomach analysis

Stomachs were opened by mid-ventral incision and the contents were removed and transferred to a 500- μ m mesh sieve for rinsing, sorting and storage in 10% formalin. Contents were blotted dry on paper towels and weighed on a MT5 Mettler Toledo balance to the nearest 0.01 mg. The stomach content of each eel specimen was examined with a binocular microscope (WILD M3Z) to identify and count ingested prey; the content was identified to the lowest taxon possible, always identified as being either aquatic or terrestrial. Ingested prey were categorised in broad taxonomic groups. The rest fractions of vegetation and digested faunal tissue were quantified as non-organismal categories.

The feeding habits of *A. anguilla* were assessed by means of the indices (Bouchereau and Guélorget, 1999):

The coefficient of Vacuity (cV) : the number of empty stomachs (N_v) in relation to the total number of stomachs examined (N_t) : $cV = 100 \times (N_v / N_t)$ (1)

Since some specimens might have digested their food during captivity in the fyke nets, empty stomachs were excluded from calculations of the indices described as:

The occurrence frequency or Percentage of Presence (PP) of prey in stomach contents : the percentage of stomachs examined containing the category of prey i (N_{ti}) in relation to the total number of stomachs containing prey (N_p) :

$$PP = 100 \times (N_{ti}/N_p) \quad (2)$$

The numeric percentage (N) : percentage of prey counted in one category i (N_i) in relation to the total number of prey counted (N_{pt}) : $N = 100 \times (N_i/N_{pt})$ (3)

Eel feeding strategy was assessed using the feeding strategy diagram of Costello et al. (1990), by plotting PP as a function of N . The two diagonals, respectively, represent the importance of prey (dominant, rare) and the predator's feeding strategy (specialist, generalist). Points around 100% PP and 1% N indicate that the predators have a specialised feeding regime. The diagonal from points close to 100% PP and 100% N (representing dominant prey) and points around 1% PP and 1% N indicates an opportunistic feeding strategy.

Diversity of ingested prey for each individual specimen was investigated using the Shannon–Wiener Index H' (Begon et al., 1990):

$$H' = - \sum_{i=1}^S (p_i \ln p_i) - [(S - 1)/2N]$$

with S , the number of prey species (species richness); N , The total number of all individuals in a stomach; p_i , The relative abundance of each prey species, calculated as the proportion of the number of individuals of a given species to the total number of individuals in the community: n_i/N ; n_i , The number of prey individuals of species i : the abundance of prey species i .

Condition

The condition factor K' for examined eel is calculated as described by Bagenal (1978):

$$K' = (100 \text{ BM})/L^b$$

with BM, weight or fish biomass (g); L , total length (cm) and b , regression coefficient of the length-weight relationship (LWR) calculated for all eels caught.

When exploring relative condition of individuals within a sample, Le Cren's (1951) relative condition factor (K'') was used as recommended by Froese (2006). K'' was calculated by dividing the individual fish biomass by the expected weight based on the length-weight relationship (Le Cren, 1951; Bagenal, 1978).

Davidson and Marshall (2010) showed that condition factors of fishes derived from length-weight relationships (K' and K'') are good indices of muscular fat content as defined by fat-meter estimates. Therefore these condition factors could be used as a good descriptor for fish condition or fatness, without the necessity of measuring individual lipid contents of captured eels.

Caloric values

Estimates of caloric values of observed prey of each individual eel were obtained from the literature (Appendix 1). Eels with

empty stomachs were excluded from the assessment. Analyses were carried out with the total caloric values while including the rest fraction (TCV_{+RF}). In a second analysis we excluded the rest fraction (TCV_{-RF}). Caloric equivalents (cal g^{-1} dry weight, ash free dry weight and wet mass) for both aquatic and terrestrial prey items of eel are summarised in Appendix 1. No wet mass caloric values are available for lepidoptera larvae, only for dry weight and ash-free dry weight (Schroeder, 1977a,b). The data given by Cummins and Wuycheck (1971) for terrestrial insects are in line with Schroeders data for lepidoptera larvae and were therefore used to calculate energy densities of ingested lepidoptera prey. Only wet mass caloric values were used to calculate energy densities of ingested prey.

Statistical analysis

Results are shown as mean values with their standard deviation (mean \pm SD). Data were checked for normality using a Shapiro–Wilks W -test. Differences in stomach content and caloric value were analysed by the non-parametric Mann–Whitney U -test ($W < 0.9$). Differences in length and condition between eels caught in the Lippenbroek and those of the River Schelde were analysed with a simple t -test, independent of the group ($W > 0.9$). In addition to the condition factor analysis we performed an Ancova with biomass as the dependent variable and total length as the co-variate to detect differences in length-weight relationships in eels from both habitats. We used logarithmic transformed data of total length and body mass (BM) for all captured eels. The significance level was taken at $P < 0.05$. Due to the relatively small sample size – which may increase the type II error rate – we also report indicative results with an alpha between 0.05 and 0.1. All statistics were conducted with STATISTICA (work package 6.0; Statsoft Inc., Tulsa, OK).

Results

Numbers and lengths of eels

In total, 85 eels were captured in the Schelde-Lippenbroek ecosystem. TL averaged 42.0 ± 11.1 cm, with a minimum length of 23.5 cm and a maximum of 76.0 cm. A total of 39 eels were used for the stomach content analysis: 15 in the Schelde and 24 in the Lippenbroek area. TL of the examined eels in the Schelde-Lippenbroek sample averaged 42.5 ± 11.2 cm, with a

minimum length of 29.5 and a maximum of 76.0 cm. Total lengths of examined eels did not differ between the Lippenbroek and the River Schelde ($W = 0.91$; $t_{37} = -1.229$; $P = 0.23$).

Stomach content analysis

Stomach content analysis revealed 31 eels with food in their stomach: 83.3% in the Lippenbroek (20/24 eels) compared to 73.3% for the River Schelde (11/15 eels). The coefficient of Vacuity was 16.7 and 26.7, respectively. Only three eels ingested food particles but had no detritus or vegetation in their stomachs (two eels in River Schelde; one eel in Lippenbroek). The number of organisms observed in stomachs ranged from 1 to 1130 for the Lippenbroek and 1 to 2877 for the River Schelde but did not differ significantly ($W = 0.31$; $z_{\text{adj}} = -0.49$, $P = 0.6$). The average number of prey items for the Lippenbroek was 94 ± 259 (4 ± 6 when the number of fish eggs was not taken into account) and 248 ± 828 for the River Schelde. Additionally, the number of ingested fish eggs in the Lippenbroek (90 ± 260) was significantly higher than in the River Schelde, where no ingested eggs were found ($W = 0.30$; $U_{20,12} = 78$; $z_{\text{adj}} = -2.26$, $P = 0.024$).

Sixteen different categories of prey were encountered (Fig. 2). Food items were distributed to a large extent among small fishes, oligochaetes, crustacea (Asellidae and Gammariidae), larvae of insects (Chironomidae) and several terrestrial organisms (Lumbricidae and lepidoptera larvae). Fishes in seven eel stomachs were digested beyond visual identification. Identifiable prey fishes included four topmouth gudgeons (*Pseudorasbora parva*), three Prussian carps (*Carassius gibelio*) and two bitterlings (*Rhodeus sericeus*). All ingested fishes were smaller than 9 cm total length.

In the River Schelde the prey consist solely of tubificids (PP = 55), fish (PP = 18) and occasionally gammarids (PP = 9). The weight percentage of gammarids is rather small compared to the other prey items in the River Scheldt (Fig. 2). In the inundated area the food eaten by eels is more diverse, consisting mostly of fish eggs (PP = 35), terrestrial lumbricidae (PP = 35) and fish (PP = 30), followed by caterpillar larvae (PP = 15), asellids, Lumbriculidae, chironomids, Hirudinea and terrestrial insects (PP = 10). Some eels had decapods or terrestrial isopods (PP = 5) in their stomachs (Figs 2 and 3).

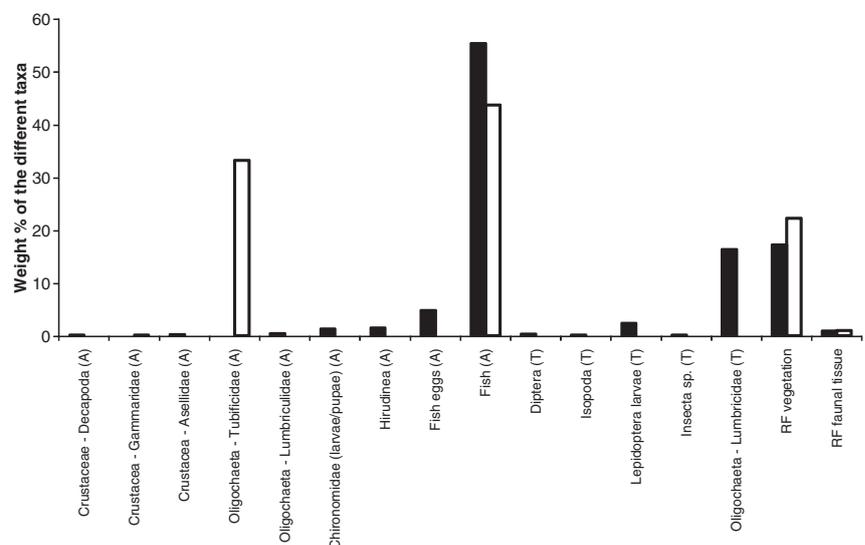


Fig. 2. Overall weight percentage of ingested eel prey/stomach contents, inundation area Lippenbroek (solid bars) vs the Schelde (open bars) (with A: aquatic prey and T: terrestrial prey)

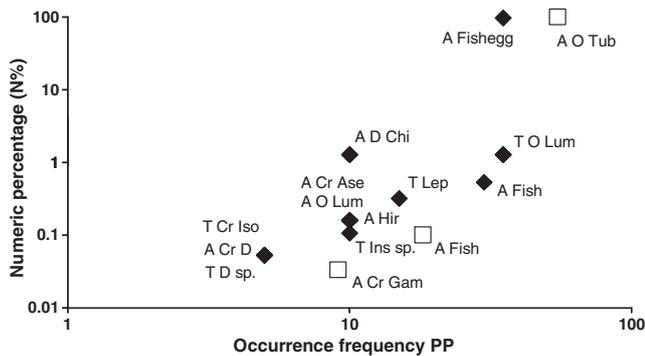


Fig. 3. Costello diagram for ingested eel prey caught in Lippenbroek area (\blacklozenge) and River Schelde (\square)

Stomach content analyses indicated that 90% of the eels ingested two or more taxa (including non-organism categories). When the rest fraction (faunal tissue or bulk vegetation) is not taken into account, 55% of the eels in the Lippenbroek still showed a mixed diet of at least two different taxa. The different number of taxa ingested by eels ranged from 1 to 9 for the Lippenbroek and 1–3 for the River Schelde where only 17% of the eels ingested more than 1 taxon (67% when taken into account the rest fraction). The average number of taxa in eel stomachs was significantly higher in the inundated flood area (1.80 ± 1.67) than in the River Schelde (0.75 ± 0.75) ($W = 0.74$: $U_{20,12} = 69.5$; $z_{\text{adj}} = -2.06$, $P = 0.04$). In the Lippenbroek, eight eels had only aquatic prey in their stomachs, five only had terrestrial prey, and four eels consumed terrestrial as well as aquatic prey (three eels had only rest fractions in their stomachs). Eels caught in the river Schelde consumed exclusively aquatic prey. For eels with food in their stomachs, the Shannon-Wiener diversity index of ingested prey showed a higher diversity in eels foraging in the Lippenbroek ($W = 0.65$: $U_{20,12} = 70.5$; $z_{\text{adj}} = 2.01$, $P = 0.04$). The ingested prey diversity of eels foraging in the Lippenbroek (0.249 ± 0.386) was about four times higher than that of eels foraging in the River Schelde (0.0598 ± 0.104).

Results of the stomach content analyses are summarised in Table 1. Stomach content weights did not differ significantly in eels of the Lippenbroek or River Schelde ($W = 0.65$:

$U_{20,12} = 71.0$; $z_{\text{adj}} = -1.91$, $P = 0.06$), although there was an indication in favour of the Lippenbroek. Our results show no significant differences in the number or weight of ingested aquatic organisms between individual eels caught in either habitat, but strong differences in the types of aquatic taxa were encountered (see Fig. 2, e.g. tubificids were ingested only by eels caught in the River Schelde, while only fish eggs were ingested by eels caught in the Lippenbroek). Furthermore, Lippenbroek eels had more large terrestrial food particles in their stomachs than did River Schelde eels ($W = 0.40$: $U_{20,12} = 66.0$; $z_{\text{adj}} = -2.66$, $P = 0.008$).

Condition

The regression of the LWR of all eels captured in the Lippenbroek and River Schelde is calculated as $BM = 0.0006L^{3.2621}$ ($R^2 = 0.9626$; $P < 0.000001$). Eels caught in the Lippenbroek (K' : 0.0665 ± 0.008 ; K'' : 1.11 ± 0.14) seemed to be in better condition than eels caught in the River Schelde (K' : 0.0625 ± 0.012 ; K'' : 1.04 ± 0.19), although the result is only indicative ($W = 0.98$: $t_{83} = 1.85$; $P = 0.07$). However, the Ancova analysis testing for differences in body mass with length as a co-variate showed that eels captured in the Lippenbroek were indeed significantly heavier for a given length than eels captured in the River Schelde ($F_{1,82} = 4.173$; $P = 0.04$).

Caloric values

For aquatic prey, caloric values ranged from 645 cal g^{-1} wet mass for aquatic annelids to 1492 cal g^{-1} for fish eggs; for terrestrial prey these values ranged from 782 cal g^{-1} wet mass for terrestrial annelids to 2315 cal g^{-1} for terrestrial insects (arthropods). Considering the different taxa, while excluding the rest fraction in the analysis, only an indicative result was found (TCV_{-RF} : $W = 0.60$: Schelde: $1588 \pm 3555 \text{ cal g}^{-1}$ and Lippenbroek: $3597 \pm 6238 \text{ cal g}^{-1}$; $z_{\text{adj}} = -1.82$, $P = 0.07$). However, considering the entire stomach contents, total caloric value of individual stomach contents of eels caught in the Lippenbroek ($4126 \pm 6369 \text{ cal g}^{-1}$) is twice as high as that of eels caught in the Schelde ($2074 \pm 4047 \text{ cal g}^{-1}$) (TCV_{+RF} : $W = 0.63$: $z_{\text{adj}} = -1.99$, $P = 0.047$).

Table 1

Results of non-parametric Mann–Whitney U test for stomach analysis of eels foraging in Schelde River (S) and eels foraging in an adjacent inundated flood area (LB), with T , number of taxa, and org, number of organisms divided in terrestrial (ter) and aquatic organisms (aqua), RF, rest fraction and sc, stomach content. Significant differences shown in bold italic and indicative results presented in plain italic

	Rank sum S	Rank sum LB	U	z	P-level	z_{adj}	P-level	Valid N, S	Valid N, LB	2*1 sided exact p
# T	145.5	382.5	67.5	-2.04	0.04	-2.14	0.03	12	20	0.04
# $T + RF$	130.5	397.5	52.5	-2.63	0.009	-2.76	0.006	12	20	0.007
# T aqua	184.0	344.0	106.0	-0.54	0.6	-0.58	0.6	12	20	0.6
# T ter	144.0	384.0	66.0	-2.10	0.04	-2.66	0.008	12	20	0.04
#org	185.5	342.5	107.5	-0.49	0.6	-0.49	0.6	12	20	0.6
#org aqua	203.0	325.0	115.0	0.19	0.8	0.20	0.8	12	20	0.9
#org aqua no eggs	230.0	298.0	88.0	1.25	0.2	1.30	0.2	12	20	0.2
# org ter	144.0	384.0	66.0	-2.10	0.04	-2.66	0.008	12	20	0.04
sc weight (mg)	149.0	379.0	71.0	-1.91	0.06	-1.91	0.06	12	20	0.06
sc weight aqua	187.0	341.0	109.0	-0.43	0.67	-0.44	0.7	12	20	0.7
sc weight ter	144.0	384.0	66.0	-2.10	0.04	-2.65	0.008	12	20	0.04
sc weight RF	172.0	356.0	94.0	-1.01	0.3	-1.01	0.3	12	20	0.3
sc weight vegetation/ plant material	138.5	389.5	60.5	-2.32	0.02	-2.66	0.008	12	20	0.02

Discussion

General behaviour and feeding strategy of eels

Examined eels from the Lippenbroek ingested aquatic as well as terrestrial prey which, according to the literature (cf. Desender and Maelfait, 1999; Frost et al., 2009), are present in freshwater tidal marshes. Eels in the Lippenbroek in spring fed on terrestrial organisms (mainly lumbricids and caterpillars), fishes and fish eggs; in the River Schelde the main prey items were tubificids, fishes and occasionally some gammarids. Stomach content analyses of Lippenbroek eels indicated that 55% ingested at least two different taxa. In contrast, only 17% of eels caught in the Schelde showed a mixed diet. These different feeding regimes suggest an opportunistic feeding behaviour (Bouchereau et al., 2006, 2009a,b). This was also supported by the observation that at least 16 different categories of food items, aquatic as well as terrestrial, were ingested by eel. Moreover, the Costello diagram did not show any evidence of a specialised feeding strategy of individual eels.

As expected, ingested macro-invertebrate taxa were found to be present in the Schelde-Lippenbroek ecosystem (Beauchard et al., submitted). Since eels adapt their diet according to the available resources offered by the ecosystem (Belpaire et al., 1992; Bouchereau et al., 2006, 2009a,b; Dörner et al., 2009), the diversity of food items in their diet is determined by the diversity of food in that particular ecosystem. Indeed, a high relative abundance of prey taxa in the Schelde estuary (Beauchard et al., submitted) was accorded to a higher numeric percentage of the ingested prey by many of the studied eels in the Schelde. This suggests that, at least in the Schelde, eels tend to prey on the most abundant food resource. However, this was only partially true for eels caught in the Lippenbroek: it seems in the CRT area that eels are preying more actively on large benthic prey instead of the highly abundant but small tubificids (Beauchard et al., submitted). Since some of these food items in stomachs of eel caught in the Lippenbroek were available exclusively in this area, we can conclude – even with the relatively small sample size – that this regulated freshwater tidal area functions as an important foraging habitat for European eel.

Based on our results we conclude that at least a part of the eel population in the Lippenbroek actively migrates into the intertidal zone to forage at flood time and retreat at ebb tide (cf. Gibson, 2003). However, eels do not often migrate from the Lippenbroek towards the River Schelde during the tidal cycle or *vice versa* (Simoens et al., 2007). At ebb tide, eels foraging in the intertidal zone of the Lippenbroek are likely to retreat into the central ditch of the Lippenbroek (Simoens et al., 2007). Therefore we can conclude that, at present, eels in the Schelde-Lippenbroek ecosystem are not likely to show a mixed foraging behaviour: eels caught in the Lippenbroek are most likely resident eels, and eels caught in the Schelde do not forage in the Lippenbroek inundation area. However, we can expect that under pristine conditions eels from the River Schelde would forage in the inundation areas (Gibson, 2003). Optimising the outlet sluices of the CRT areas, allowing eels to swim freely in and out the inundation areas, could therefore optimise the eel feeding strategy.

Prey diversity related to habitat diversity

Archambault and Bourget (1996) showed that species richness and macro-invertebrate abundances increase with heterogene-

ity. It is generally accepted that intertidal areas harbour high habitat diversity (Davidson et al., 1991); in fact, intertidal areas and flood plains are often more diverse than the main stream itself. More diverse food resources are available to eels that can use the freshwater tidal inundation area, thus this area may offer important additional food resources for the European eel. Keiper et al. (2002), Maris et al. (2008) and Frost et al. (2009) showed that inundation areas are characterised by a larger taxonomic richness of macro-invertebrates compared to the main river, and Desender and Maelfait (1999) found a higher diversity of terrestrial species in tidal marshes along the Schelde estuary. Obviously, it is difficult to assess integrated effects of feeding in the main river system or intertidal area by a 2-day sampling expedition in spring; differences between neap/spring tides, day and night cycles, lunar cycles or seasons remain to be investigated. The sampling covers only a short period of the year and, for certain, it would have been better to take samples over the entire eel feeding activity period from spring to late autumn for eels of temperate Europe (Tesch, 2003). Our results do not allow formulation of clear conclusions for other periods; however, our examination of the diet in eels foraging in the Lippenbroek-Schelde ecosystem clearly supported the findings of several authors (Archambault and Bourget, 1996; Keiper et al., 2002; Maris et al., 2008; Frost et al., 2009; Beauchard et al., submitted) that inundation areas are characterised by a larger taxonomic richness of macro-invertebrates and that they support a higher diversity of terrestrial species.

Taking into account the number of fish eggs ingested by eels in the Lippenbroek area, fish eggs are obviously an important additional springtime food source in the inundation area. Simoens et al. (2007) found, among other fish species, high densities of three-spine sticklebacks in the shallow northern water body of the Lippenbroek; Bergersen and Klemetsen (1988) showed that eels frequently eat complete stickleback nests with eggs. This may also partially explain the higher amount of vegetation as rest fraction in the stomachs of eels foraging in the controlled inundated area.

Energetic consequences

Differences in stomach contents between sites could be caused by the specific digestion rates of prey, resulting in a different probability for a certain prey item to be found in the samples, which in turn could influence the caloric value estimates. Studies on different digestion rates of prey in eel are scarce, but one study estimated a general digestion rate of 3–4 h for elvers (Belpaire et al., 1992). In our study, eel stomachs were sampled within the time frame where the degree of fullness is > 50% (Belpaire et al., 1992), assuring that most prey items were still present. Moreover, stomachs and guts were removed *in situ* and immediately fixed in 10% formalin, stopping further digestion. Since both habitats were sampled simultaneously, differences in stomach contents and caloric values are likely to reflect relative differences between habitats.

Our results show that the total caloric value of the ingested prey of eels caught in the Lippenbroek in spring was twice as high as those of eels caught in the River Schelde. Consequently, eels foraging in the Lippenbroek – feeding on aquatic as well as (high calorically) terrestrial prey – may have an energetic advantage over eels foraging in the river. Although no significant differences were found in condition factors between the two groups, the P-values were close to

0.05. Moreover, the covariance analysis showed significant differences between both habitats, suggesting that the energetic advantage is effectively converted into a higher body mass in the Lippenbroek area. This energetic advantage might be important to establish measures for the recovery of the stock of European eel. Indeed, Belpaire et al. (2009a) suggested that the decrease in fat content in yellow eels is probably a key element in the stock decline. When spawner quality is poor and the lipid content low, silver eels may not contribute to the overall spawning (Belpaire et al., 2009a). In Flanders, eel seems to be at an overall poor level of quality (Belpaire et al., 2009b), emphasising the importance of diverse food resources. Infections by parasites (Kelly et al., 2000; Kirk, 2003; Sures et al., 2006), viruses (Van Ginneken et al., 2005; Jakob et al., 2009), or hazardous substances (Palstra et al., 2006; Belpaire and Goemans, 2007; Geeraerts and Belpaire, 2010) could certainly have a noticeable impact on the reproductive potential of eels. However, we should also consider that high fat levels in eels are of crucial importance as energy sources to complete the eel reproductive cycle (Belpaire et al., 2009a).

Eels collect energy from the available food for storage as lipids in muscles and internal organs. Bergersen and Klemetsen (1988) showed that 75% of the silver eels have at least 20% fat in the somatic muscle tissue. Normally, fat reserves of eels are between 26 and 30% of their body weight (Bergersen and Klemetsen, 1988; Van den Thillart et al., 2007). However, in 2004 yellow eels in Belgium appear to have a mean lipid content varying between 2.0% and 23.4%, with a mean of only 12.7%. Moreover, a significant 7.7% decrease in the lipid content over the last 13 years was observed in Belgian eels (Belpaire et al., 2009a). Further, Lasne et al. (2008) showed in downstream river segments that eels had lower condition in disconnected waterbodies than in connected ones. They explained the higher body condition of individuals as the result of the proximity of brackish waters, which probably provides good environmental conditions for eel growth. However, based on our results, we assume that movement in and out the intertidal zone increases the food intake of eels, also hypothesised by Gibson (2003) for marine species. In some species, like herring, fat reserves indicate the feeding conditions experienced by the fish, being high when food is plentiful and low when food is scarce (Wood, 1958). Whether food availability affects lipid content in eel is poorly understood, but it was reported that under culture conditions, lipid content in eels can be influenced by the energy content of the food provided (Garcia-Gallego and Akharbach, 1998). Our results show that the number and biomass of aquatic organisms ingested by eels in spring is the same in both the Lippenbroek and Schelde. However, eels foraging in the Lippenbroek area had consumed significantly more terrestrial prey, resulting in increased total stomach content. Eels in the inundation area have access to more diverse prey; even more important, they consume prey with higher calorie content. As a result, yellow eels caught in spring in the inundation area are heavier for a given length than yellow eels caught in the River Schelde, and are therefore assumed to be fatter and healthier than eels caught in the main river system.

Intertidal areas as important habitats for eel

Belpaire et al. (2009a) hypothesised that a decrease in lipid content as observed in yellow eels is indicative of a similar

proportional decrease of energy reserves in the silver eel. Thus we can assume that eels foraging in the inundation areas (CRT) during their yellow eel stage could have higher energy reserves when silvering and in the end stage of the spawning migration. They are therefore more likely to contribute to the brood stock than eels solely foraging in the main river system. Specifically, lipid reserve in the silver eels is not only accumulated for its trans-oceanic migration but also for the later formation of gonads (Boëtius and Boëtius, 1985; Jonsson and Jonsson, 2005). It has been suggested that fat content is a key factor triggering migration (Larsson et al., 1990; Svedäng and Wickström, 1997) since reserves have to be sufficient to overcome the 5500 km migration route towards the spawning grounds in the Sargasso Sea. However, Svedäng and Wickström (1997) found that silvering and spawning migration may also begin at low fat concentrations; nevertheless, they hypothesised that it is highly unlikely for silver eels with really low fat reserves ever to contribute to the next generation. Therefore the migration process is likely to be temporarily put on hold, and feeding could be resumed (cf. Dollerup and Graver, 1985). This leads towards a semi-yellow stage, avoiding the death of lean eels or that they will lose their ability to spawn en route to the spawning grounds (Svedäng and Wickström, 1997). Silvering eels with low fat content could resume feeding in high quality feeding grounds such as intertidal freshwater inundated areas, which could function as some sort of waiting room for eels that are not ready to fulfil their reproductive cycle. Moreover, it is also worth mentioning that a better quality of foraging habitat may increase the turnover of generations due to faster maturation (Svedäng et al., 1996).

Starkie (2003) suggested that improving degraded natural surface waters to meet the Water framework Directive could, in turn, lead to an improved stock of European eel. Our results indeed suggest that reconnecting freshwater floodplains, even freshwater areas of controlled reduced tide specifically developed for flood control, can be important, which is also in accordance with Lasne et al. (2008) who suggested that rehabilitation of downstream floodplains of large river systems are of great importance for the species. At a basic level, more qualitatively better yellow eels can be expected to produce more silver eels (Bark et al., 2007). In accordance with the European plan for recovery of the eel stock, in 2008 an Eel Management Plan was developed for Belgium, aiming at a silver eel (spawner) escapement of 40% in biomass terms, relative to the pristine state. By reconnecting large-scale inundation areas, the percentage of qualitatively better silver eels with higher lipid content (fatter eels) might increase significantly.

Our results clearly show the importance of the inundated areas as foraging habitat for the European eel. Moreover, analysis of ingested prey revealed circumstantial evidence that areas of controlled reduced tide could also act as important spawning grounds for freshwater fish species. The number of fish eggs in the stomach of eels compared to the absolute absence of fish eggs in the eels caught in the River Schelde shows the importance of tidal areas for spawning. This function is also often suggested by various authors (e.g. Maes et al., 2005; Simoens et al., 2007; Breine et al. (2009)), mostly without the supporting data. This study shows that freshwater estuarine inundation areas are very important feeding as well as spawning habitat for freshwater fishes in the Schelde estuary.

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Appendix 1

Caloric equivalents (cal g⁻¹ dry weight, ash free dry weight, wet mass) for aquatic (bold) and terrestrial (italics) prey items of eel, Lippenbroek – Schelde ecosystem.

Taxon	Dry weight (cal g ⁻¹)	Ash-free dry weight (cal g ⁻¹)	Wet weight (cal g ⁻¹)	Ref
Osteichthyes	5086	5296	1493	a
Cyprinidae	5761			a
Common carp			857	b
Prey fish			1166	b*
Salmonidae (eggs)	3598	3736	1492	a
Annelida	3910	4700	645	a

Taxon	Dry weight (cal g ⁻¹)	Ash-free dry weight (cal g ⁻¹)	Wet weight (cal g ⁻¹)	Ref
Tubificidae	5652		760	a
Lumbriculidae	4833			c*
Erpobdellidae	5443			a
Nepheleopsis obscura (leeches)	5344			e
Arthropoda	4726	5445	792	a
Amphipods sp.	3761		1058	a
Gammaridae	4050	5362	810	a
Asellidae		4325		a
Decapoda	3944	5314	1077	a
Chironomidae	5424	5355	656	a
<i>Invertebrates</i>	5274	5673	2008	a
<i>Annelida</i>	4569	5628	782	a
<i>Lumbricidae</i>	5012	5628	782	a
<i>Arthropoda</i>	5289	5673	2315	a
<i>Isopoda</i>	3786			a
<i>Oniscidae (terr. isopoda)</i>	4197			a
<i>Insecta</i>	5454	5703	2315	a
<i>Diptera</i>	5783			a
<i>Diptera larvae (sarcophagidae)</i>	5914			a
<i>Lepidoptera larvae</i>	5800	6000		d
<i>Phragmites australis</i>	4077			f*
<i>Phragmites australis</i>	4200		1000	g*

Sources: a. Cummins and Wuycheck (1971). b. Bryan et al. (1996), *weighted mean for prey fish, derived from Bryan et al. (1996). c. *weighted mean derived from Hansen et al. (2004). d. Schroeder (1977a). e. Driver (1981). f. *Mean caloric value derived from de la Cruz (1983). g. *Wet weight caloric value recalculated from Yanling et al. (1988) using energy conversion factor of 4.2 kcal g⁻¹ dry weight suggested by Leith and Whittaker (1975) for wetland vegetation.