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Freshwater protected areas: an effective measure to reconcile conservation and exploitation of the threatened European eels (*Anguilla anguilla*)?

Cucherousset J, Paillisson J-M, Carpentier A, Thoby V, Damien J-P, Eybert M-C, Feunteun E, Robinet T. Freshwater protected areas: an effective measure to reconcile conservation and exploitation of the threatened European eels (*Anguilla anguilla*)?
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Abstract – For decades, the European eel *Anguilla anguilla* (L.) population has been declining strongly despite several management attempts, so additional experiments need to be conducted on management measures. The use of freshwater protected areas has been advocated but their efficiency has never been assessed. In this study, we investigated whether the population structure and the silver eel (mature migrating stage) production differ in fished and protected areas within a marsh wetland (Brière, 7000 ha, Northwest France), using an intensive biological study (electrofishing and trapping) and a survey of the traditional fishery (licenses, questionnaires and creel surveys). First, we found that fishermen mainly targeted >320-mm yellow eels (sedentary stage) using pots and square dipping nets and that harvest by fishermen was highly variable at different locations in the study area. Secondly, we found differences in the size-class structures and mortality rates between protected and fished areas. Mortality rates of eels >320 mm was positively correlated with harvest by fishermen. Furthermore, the proportion of potentially migrating eels in the total population was found to be higher in the protected areas than in fished areas (6.38% vs. 1.42%, respectively). Thirdly, we found that protected areas potentially produce 8.4% of the total silver eel production whereas they only account for 2.4% of the aquatic habitat area. We estimated that a size adjustment of protected areas to 31.1% with maintaining the current fishery would produce 50% of the potential silver eel of a fully protected marsh. Protection of freshwater areas appears to be a promising management measure and a constructive consensual way to integrate the patrimonial and societal value of the traditional fishery and the international management plans for European eels. Furthermore, freshwater protective measures can be an effective local solution if they are integrated into the framework of freshwater biodiversity management and accompanied by other management measures that focus on all eel life stages.

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Key words: *Anguilla anguilla*; spawners production; protected area; habitat restoration; coastal freshwater marsh

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Introduction

The European eel *Anguilla anguilla* (L.) population is in steep decline that began in the 1970s (Moriarty & Dekker 1997; Feunteun 2002; ICES WGEEL 2006). The most frequently cited causes for the decline are: global warming and its effects on marine currents and ocean productivity, obstructions to migration,

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fisheries, habitat degradation and parasite infestations (Feunteun 2002; Robinet & Feunteun 2002; Starkie 2003). Attempts to manage and restore local stocks include (see review in Feunteun 2002) (i) regulation of fisheries at various biological stages (e.g., Rosell et al. 2005); (ii) management of obstacles to migration in particular fish passes (e.g., Knights & White 1998) and (iii) restocking programmes (e.g., Moriarty & Dekker 1997). Despite all these programmes, the general decline continues, and additional management measures need to be developed. Since 1999, the ICES Working Group on Eel has recommended reducing anthropogenic impacts on the production and escapement of silver eels (i.e., mature migrating stage) to the lowest possible levels (ICES WGEEL 2006). Now, the situation is becoming increasingly critical for the eel fisheries, and ICES experts expressly demand to identify ‘areas producing high quality silver eels (large sized females, low contaminant and parasite burdens, unimpacted by hydropower stations)’, to prioritise their conservation (ICES WGEEL 2006). Concrete actions must now be focused on the quantity and quality of the future silver eels leaving freshwaters (Dekker 2003).

Marine protected areas have been proposed as an easily enforced conservation method for managers to reduce the impacts of fishing on marine populations and habitats (Apostolaki et al. 2002). Scientists have developed practical and theoretical approaches for the design and the implementation of marine protected areas that have benefits for biodiversity and fisheries threatened by anthropogenic activities (see review in Leslie 2005). Recent research has shown that the success of marine protected areas also depends on the integration of social, economic, political and scientific factors (Lundquist & Granek 2005; Stem et al. 2005). Some attempts have been recently conducted worldwide, with variable success, to develop freshwater protected areas (Maitland 1995; Keith 2000; Saunders et al. 2002). Few areas have been created specifically for freshwater fish, and almost all freshwater protected areas were included ‘incidentally’ as part of terrestrial reserves (Eybert et al. 1998; Keith 2000; Self 2005). Although freshwater protected areas have been advocated for the management of American and European eel stocks (Feunteun 2002; Morrison & Secor 2003), their utility for conservation has not been evaluated.

Small freshwater coastal marshes are useful for studying this issue because they are widely colonised by eels (Feunteun et al. 1992) and in recent decades, habitat restoration programmes have been undertaken and in some cases, freshwater protected areas were created. These ecosystems also comprise recreational and traditional eel fisheries and their limited size allows the whole local eel population to be studied. Furthermore, the role played by many small inland ecosystems in terms of the silver eel production remains to be quantified (Feunteun et al. 2000). The configuration of the Grande Brière Mottière (GBM, western France) offers good opportunities to test the efficiency of protected areas for eels because this coastal freshwater marsh has a traditional fishery and two protected areas that were created in the early 1980s.

Based on a data set, combining both a scientific investigation in the field and a traditional fishery survey, the objectives of the present study were (i) to characterise the yellow eel (i.e., sedentary stage) size-classes targeted by the local fishery and the spatial distribution of catches; (ii) to compare the eel population structure between fished and protected areas by analysing size-class distributions, mortality rates and silver eel production; (iii) to measure how the fishery impacts the eel size-class structure and finally (iv) to estimate the local eel stock and the differences in silver eel production to evaluate the efficiency of protected areas on the quantity and quality of the future silver eels leaving the GBM.

Materials and methods

Study area

The GBM is a freshwater and coastal wetland marsh of 7000 ha that flows in the Loire River estuary (North West France, 47°22′N, 02°11′W). The aquatic habitat is composed of a complex network of permanent ditches (144-km representing 206.4 ha) and semi-permanent ponds (392.7 ha) within a patchwork of temporary flooded wetlands composed of grasslands and reed beds (Fig. 1). In the general framework of restoration programmes developed in the early 1980s to limit the expansion of reed beds (Bernard & Rolland 1990), two protected areas where fishing, hunting and entry are totally prohibited, have been created (Eybert et al. 1998, Fig. 1). The southern and northern protected areas were created in 1973 and 1989, and cover 700 and 250 ha of land composed of 8.1 and 6.5 ha of aquatic habitat, respectively. Based on traditional habits, the study site is divided into eight zones where fishing is permitted, plus the two protected areas (Fig. 1).

Traditional fishery survey

Data from the traditional fishery survey were used to estimate the targeted eels’ sizes, the fishing efforts and the fishery harvest from questionnaires. Since 1784, the GBM marsh had its own property law (‘undivided’ and privately owned) and a specific fishery legislation, the fishery being composed of noncommercial fishermen. In this marsh, no minimum legal size regulation

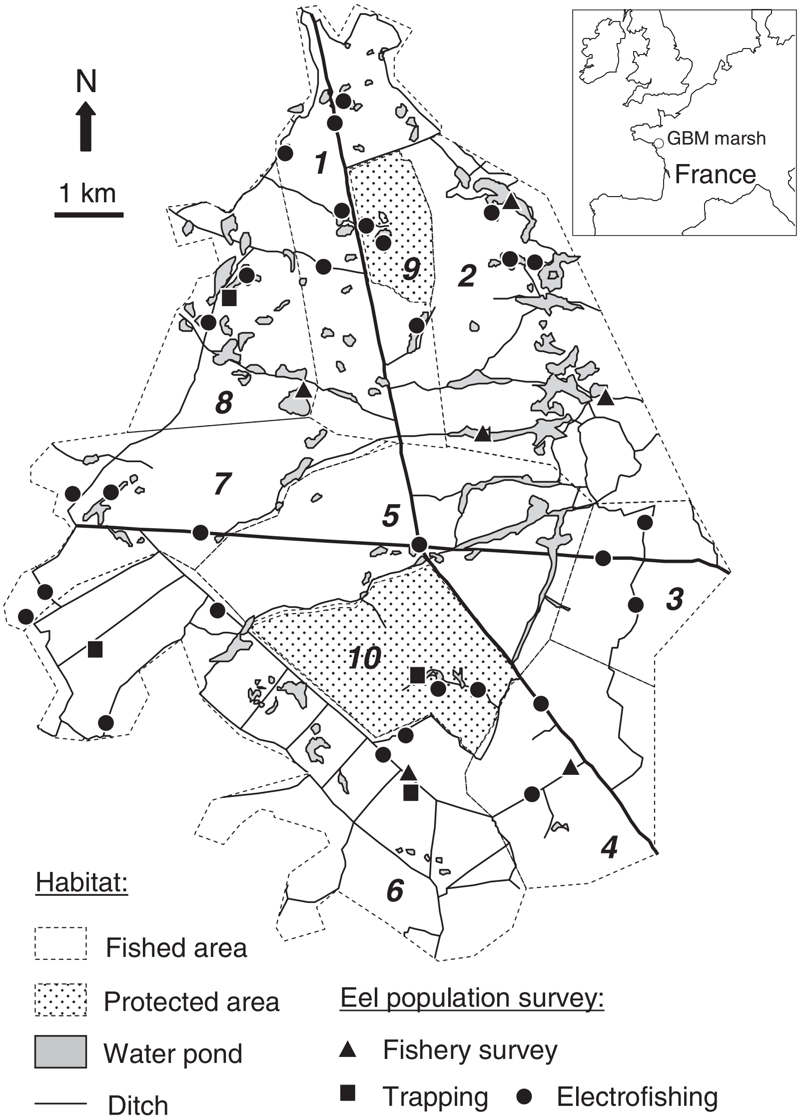

Fig. 1. Map of the Grande Brière marsh illustrating the ditch network, ponds, fished and protected areas with their codes and the location of eel population surveys: fishery survey (▲), trapping (■) and electrofishing (●) during 2004 and 2005.

exists. In 2005, a fishery survey was conducted to assess the harvest by fishermen (expressed as the number of eels captured per ha) for each type of gear at different zones of the study area (Fig. 1) using three different methods. First, all fishing licences were analysed to count the number of fishermen and to assess the total number of gear used [product of the number of fishermen with the mean (±SE) number of each gear per fishermen]. Secondly, anonymous questionnaires were distributed to evaluate the fishing practices as logbooks were rarely available. During the fishing season, questionnaires were randomly distributed directly to fishermen in the field or via fishermen associations. Follow-up contacts were made to improve the response rate. Fishermen were questioned on the species targeted, their catches, the number and type of gear and the frequency and location of their trips. Representativeness of the questioned fishermen was checked to ascertain the wider application of the data (Roth et al. 2001) by comparing these fishermen to the total fishing licences using a chi-square test. Thirdly, some fishermen were accompanied during their trips (creel survey) to assess the size-classes targeted by comparing the total captures with those fish released. Based on the fishermen logbooks available ($N = 3$), we found that eel captures occurred mainly in May (73% of total captures) as a result of a very limited seasonal efficiency of fishing gears with respect to the local water regime. Based on questionnaires, we calculated the number of eels caught during this month by multiplying the number of fishermen with the mean (±SE) number of each gear per fishermen and with the mean (±SE) catch per unit effort (CPUE) for of each gear and then, the total

Table 1. Sampling design of the eel population and traditional fishery surveys in protected and fished areas of the Grande Brière Mottière marsh in 2004 and 2005.

Method	Year	Area	Period	Habitat	Number of sites	Sampling effort	Number of eels
Electrofishing	2004	Fished	August	Ditch	15	25.1 PAS/site	244
		Protected	August	Ditch	2	31.5 PAS/site	21
	2005	Fished	June–July	Ditch	17	25.0 PAS/site	304
				Pond	9	27.8 PAS/site	68
		Protected	June–July	Ditch	2	25.0 PAS/site	25
				Pond	2	30.0 PAS/site	19
Trapping	2004	Fished	June–July	Ditch	3	Eight gear	125
		Protected	May–August	Ditch	1	Ten gear	449
	2005	Protected	March–August	Ditch	1	Ten gear	347
Fishery survey	2005	Fished	March–June	Ditch	6	13 fishing trips	266

number of catches was extrapolated from the survey results for the whole year.

Eel population survey

Sampling

The eel population was sampled in 2004 and 2005 using trapping and electrofishing (Fig. 1 and Table 1). Trapping at randomly chosen locations was used to assess population parameters (i.e., size-class profiles, proportion of silver eels and sex ratio) in restricted locations of the protected and fished areas. It was conducted using fyke nets (two wings 1.2-m high and 3-m long directing the fish into the 2-m long and 50-cm diameter chamber of 5-mm mesh) and fishermen eel pots (1.5-m long with 1.0 × 0.4-m frames and 10-mm mesh). All trapping data (fishermen creel and scientific surveys) were pooled to increase the number of eels sampled (Table 1). Because trapping was not applicable to the whole study area, electrofishing was randomly conducted at different locations over the whole study area in 2004 and 2005 to assess the geographical variation in eel abundance (Fig. 1 and Table 1). Sampling was conducted with an EFKO F.E.G. 8000 apparatus (Leutkinch, Germany) using the point abundance sampling method (PAS; Nelva et al. 1979), with the PAS number per site being in accordance with Persat & Copp's (1989) recommendations. Indeed, PAS is an efficient and cost-effective method for assessing fish abundance and population structure and provides reproducible and quantitative samples that allows within- and between-sites comparisons (Copp 1989). In total, we conducted 1225 PAS in 17 and 30 sites sampled in 2004 and 2005, respectively (details in Table 1). Abundance was expressed in CPUE, i.e., the number of eels caught per PAS.

For the two sampling methods, eels were anaesthetised with eugenol (0.04 $ml \cdot l^{-1}$), measured [total length (TL) to the nearest mm], weighed (*W*, to the nearest *g*), macroscopic silvering criteria were assessed (Acou et al. 2005), and then the eels were released into the water. Given that some differences might occur in the selectivity of trapping gear in relation to different mesh sizes, only eels longer than the modal body size (i.e., TL = 320 mm) were used for further analyses (Naismith & Knights 1990a,b; Knights et al. 1996). Given that elvers (postlarval stage, <150 mm, $N = 32$) have only colonised the drainage during the current year and have a higher downstream abundance, they were removed from the data set obtained by electrofishing to avoid any biases in the analyses. Where nonparametric tests showed no difference, data collected in 2004 and 2005 were combined with respect to the sampling method (trapping and electrofishing).

Population parameters

The total mortality rate per year (Z) was calculated in the protected and fished areas, using the age-size relationship established in a nearby and very similar ecosystem (at 60-km distance in Grand-Lieu lake; Adam 1997). Assuming that Z remains constant throughout the life of the cohort and that the population is in a state of equilibrium, Z was calculated for fish under full exploitation (i.e., individuals submitted to the fishery age from 5 to 7 without seaward emigration, using the following formula; see Sparre & Venema (1998) for details):

$$N_{(\text{age}=7)} = N_{(\text{age}=5)} \times e^{(-Z \times t)} \quad (1)$$

where $N_{(\text{age}=5)}$ is the number of individuals of age 5 entering the fully exploited phase, $N_{(\text{age}=7)}$ is the number of individuals of age 7 (end of the fully exploited phase), t is the time in year, and Z the total mortality rate expressed in percentage of individual per year. The mortality rate calculation was performed at the study area scale (i.e., protected vs. fished areas), and not for each zone, given the insufficient number of individuals sampled in each zone. At the zone scale, mortality was estimated by calculating the difference in abundance obtained by electrofishing (expressed in CPUE) between untargeted and targeted eel size classes.

In 2005, the proportion of silver eels was determined, using a standardised method based on macroscopic criteria (ocular index, state of differentiation of the lateral line and colour contrast) that provides a quick identification in the field of premigrant eels in a standardised way and without sacrificing any individuals (Acou et al. 2005). However, this method was applied to data collected later in the season (i.e., September and October, Acou et al. 2005), so we used two earlier criteria of silvering prior to this (i.e., ocular hypertrophy and differentiation of the lateral line). Indeed, the typical pigmentation of silver eel occurred generally at the end of the silvering process (Acou et al. 2005; Durif et al. 2005). Because few silver eels were sampled in protected area by electrofishing, the proportion of silver eels in the protected areas was calculated using the proportion of silver eels in fished area multiplied by the silvering ratio between protected and fished areas. In addition, we used the Fulton's condition factor ($K = W \times TL^{-3} \times 100\,000$) as a general indicator of premigrant quality (EELREP 2005), and used the 440-mm threshold to assess the sex of silver eels as no individuals were sacrificed during the study. Individuals longer than 440 mm are known to females (Tesch 2003; Acou et al., in press). The sex ratio was expressed as the proportion of males among premigrant eels.

Stock assessment, fishery mortality and silver eel production

The assessment of eel stocks in extensive areas is particularly difficult. Indeed, the most common technique (depletion sampling associated with electrofishing) consumes manpower and time and, thus, is not easily applicable in extensive areas (Lobon-Cervia & Utrilla 1993). Nevertheless, a method has been developed to point sample the eel abundance in freshwater areas by establishing the relationship between PAS and depletion samples (Laffaille et al. 2005a). These authors recommended developing a single relationship for each type of equipment and habitat (Laffaille et al. 2005a). Furthermore, the authors found that this relationship is linear at variable eel densities (expressed as the number of eel·100·m^{-2}, Laffaille et al. 2005a). Using the habitat differentiation between the shoreline and open water (Broad et al. 2001; Schulze et al. 2004), we established the following relationship in a typical ditch of the Brière marsh based on 25 PAS distributed in two sites sampled by depletion:

Eel density (in eel·100·m^{-2}) = 10.59 (±1.55 SE) Eel relative abundance (in CPUE from PAS).

No differences in the size-class distribution of eels between PAS and depletion sampling were found (Kolmogorov–Smirnov two-sample test, KS = 0.201, $P > 0.602$, $N = 57$). Eel stock assessment was derived from this relationship and the estimation of the area of each type of habitat (shoreline and open water) using a Geographical Information System (source Parc naturel regional de Brière).

Next, we used the mortality rates estimated in protected and fished areas and the estimated eel stock under exploitation (eels > 320 mm, see Results section) to evaluate the fishing mortality based on scientific data. We used the formula:

$$Z = F + M \quad (2)$$

where Z is the total mortality, F is the fishing mortality and M is the natural mortality, and making the assumption that recruitment and population parameters were similar in 2004 and 2005 (see section on Population parameters). Thus, in the protected areas, the fishing mortality was assumed to be zero ($F = 0$) and thus resulting in $M = Z$. For the calculation of F at the fished areas, the M-value was subtracted from the Z-value to obtain the fishing mortality ($F = Z - M$). The number of eels caught by the fishery (N_F) was estimated, using the following formula and equations (1) and (2):

$$N_F = N_{(age=5)} \times (1 - e^{[-t \times (F+M)]}) \times [F/(F+M)] \quad (3)$$

where N_F is the number of eels that died from fishing mortality, $N_{(age\,=\,5)}$ is the number of individuals of age 5 entering the fully exploited phase and t is the average number of years an eel is experiencing exploitation (i.e., 3 years). Next, estimated N_F was compared qualitatively to the results obtained from fishermen's questionnaires. Finally, silver eel production was derived from the estimated eel stock and the proportion of silver eels in both protected and fished areas. All estimates (the number and biomass of the eels) and their upper and lower values (in parentheses) resulted from the products of the lower values (mean − SE), the mean and the upper values (mean + SE) of the population parameters.

Results

The traditional fishery

A total of 521 fishing licences were sold in the GBM marsh in 2005: 34 for the use of eel pots, 66 for square dipping nets and 46 for fish spears; the rest of the licences being attributed for gill nets, rods and multiple gears. Nevertheless, gillnets and rods are principally used to catch piscivorous fish (northern pike *Esox lucius* and pikeperch *Sander lucioperca*). The eel fishery was composed of 48 fishermen using pots, 87 using square dipping nets and 60 using spears. In total, 75 fishermen responded to the questionnaires and provided data, including 28 using pots, 43 using square dipping nets and 26 using spears (i.e., approximately one-half of the total number of fishermen for each gear). Furthermore, the set of fishermen that responded to the questionnaires

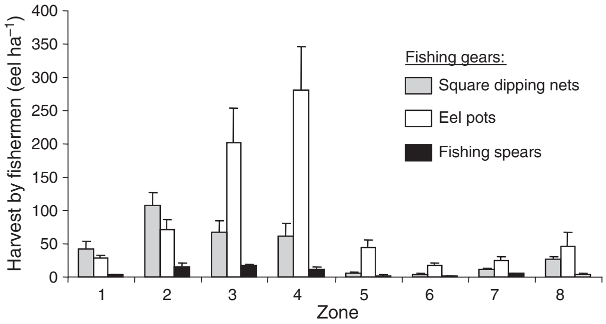

Fig. 2. Geographical distribution of the harvest by fishermen (eel·ha^{-1}) in each zone of the fished area and for each eel fishing gear (eel pots, square dipping nets and fishing spears).

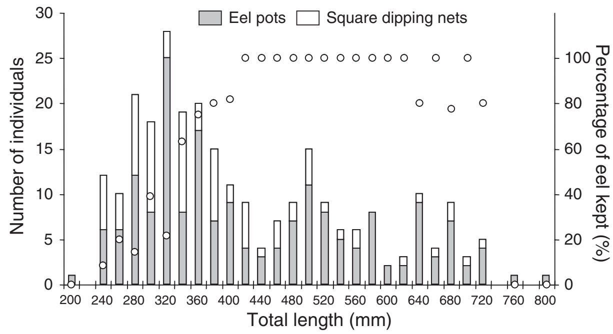

Fig. 3. Size-classes distribution of eels caught by fishermen during the creel survey using eels pots ($N = 184$) and square dipping nets ($N = 82$) and percentage of eels kept by fishermen for each size-class (white dots).

did not differ significantly from the whole eel fishery (chi square, d.f. = 2, $\chi^2 = 0.797$, $P < 0.671$). Based on these questionnaires, we estimated that 23 892 eels (18 206–29 578 ranging from lowest to highest estimation) were caught in 2005. Given that the mean weight of eels kept by fishermen was 127.7 g (±5.7 SE), the estimated total biomass of eels kept was 3052 kg (2222; 3947).

Based on the spatial distribution of the fishing activity, we found that the harvest by fishermen (in eel·ha^{-1}) varied largely between zones and gears (Fig. 2). The highest harvest by fishermen was found in the southern part of the GBM (zones 3 and 4) for all gear types, and the northern part of the GBM (zones 1 and 2), which was mainly fished with pots. The lowest harvest by fishermen occurred in the eastern part (zones 5, 6, 7 and 8; Figs 1 and 2). Because fish spears accounted for a restricted part of the catches (5%), data related to this gear have been removed from the analysis of targeted eel size-classes per gear type. Based on creel surveys, fishermen using pots and square dipping nets caught eels from 240 to 760-mm TL and 33.5% of the total eel captures ($N = 257$) were released by fishermen. The size distribution differed between released and kept eels (Kolmogorov–Smirnov two-sample test, KS = 0.678, $P < 0.001$) and released individuals were, on an average smaller than those kept (Mann–Whitney test, $U = 13.950$, $P < 0.001$). Fishermen released on an average 79.4% (±5.1 SE) of the smaller eels (240–320 mm) and kept a high ratio (up to 60 %) of eels measuring more than 320 mm. From 420 to 620 mm, all eels (100%) were kept. Interestingly, some fishermen tended to release some of the larger eels (Fig. 3). Thus, based on their size, eels were classified into those untargeted and targeted by the fishery using the 320-mm threshold.

Eel population characteristics

In 2004 and 2005, we captured 1868 eels: 681 by electrofishing, 921 by trapping and 266 during the fishermen creel surveys (see Table 1 for details). There was no difference in the size-class distribution between 2004 and 2005 for the eels sampled by trapping and by electrofishing (Kolmogorov–Smirnov two-sample test, $P > 0.05$) or in the mean abundance per site by electrofishing (Mann–Whitney test, $P > 0.05$). Eels up to 320-mm sampled by trapping in fished areas were on average smaller than those from protected areas (Mann–Whitney test, $U = 63.853$, $P < 0.001$, $N = 891$) and size-class distribution differed significantly between protected and fished areas (Kolmogorov–Smirnov two-sample test, KS = 0.164, $P < 0.001$, $N = 891$, Fig. 4). Based on the data collected by trapping and using equation (1), we found different mean mortality rates Z between protected and fished areas, 12%·year^{-1} and 32%·year^{-1}, respectively (Fig. 4). We also found that the differences in abundance between untargeted (TL < 320 mm) and targeted (TL > 320 mm) eels were positively correlated with the harvest by fishermen from protected to highly fished zones (linear regression, $R^2 = 0.51$, $P = 0.021$, $N = 10$, Fig. 5). Based on the data collected by trapping, we found that the proportion of silver eels was higher in protected than in fished areas (Fisher's exact test, $P = 0.003$). Indeed, 12.83% of eels > 320 mm ($N = 265$) caught in protected areas

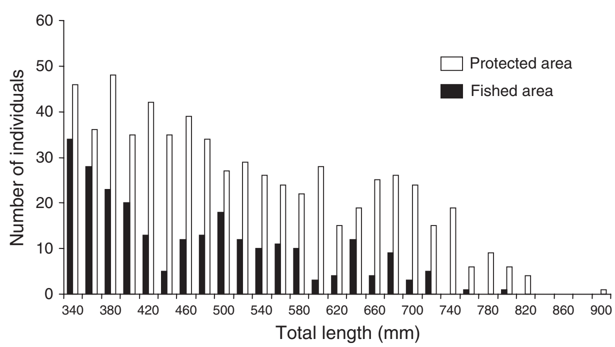

Fig. 4. Size-classes distribution of >320-mm eels trapped in fished ($N = 251$) and protected ($N = 640$) areas in 2004 and 2005.

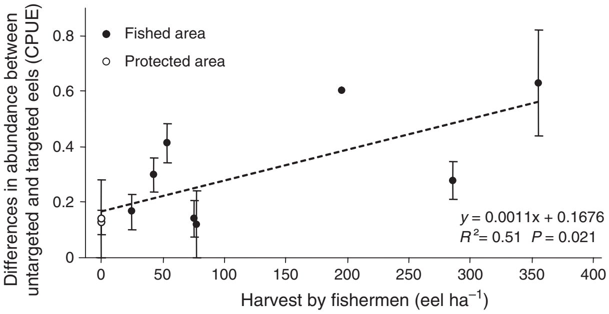

Fig. 5. Relationship between harvest by fishermen (eel·ha^{-1}) in each zone of the study area and the differences in abundance between untargeted (TL < 320 mm) and targeted (TL > 320 mm) eels.

Table 2. Number of eels and silver eels (males and females) caught by electrofishing and trapping in 2005 in the protected and fished areas of Grande Brière Mottière marsh. See details on sampling procedure and effort in the text.

Sampling method	Parameters	Fished area	Protected area	Total
	Total number	282	24	306
	Silver eels	4	1	5
	Males	0	0	0
Electrofishing	Females	4	1	5
	Total number	105	265	370
	Silver eels	3	34	37
	Males	0	1	1
Trapping	Females	3	33	36

presented silvering criteria (i.e., ocular hypertrophy and differentiation of the lateral line) whereas only 2.86% ($N = 102$) presented these criteria in fished areas. Thus, the proportion of silver eels was 4.5 times higher in protected areas than in fished areas. The proportion of silver eels in eels >320 mm in length did not differ in fished area between data from electrofishing (4.65%, $N = 86$) and trapping (Fisher's exact test, $P > 0.5$). The proportion of silver eels was 1.42% (i.e., four of 282) when all size classes from electrofishing were used in the fished areas (Table 2). The proportion of silver eels in the protected areas reached 6.38%. The sex ratio of silver eels was largely biased towards females: one of 37 by trapping and zero out of five by electrofishing, with no differences between fished and protected areas and sampling methods (Fisher's exact test, $P > 0.05$, Table 2). Silver eels had an average weight of 585.4 g (±46.8 SE, $N = 29$), a mean length of 675.8 mm (±17.5 SE), and a mean condition factor 0.18 (±0.01 SE).

Stock assessment, fishing mortality and silver eel production

The mean estimated eel density was highly variable between zones (234.2 ind·ha^{-1} ± 42.4 SE), ranging from 94.1 to 577.0 ind·ha^{-1}. The overall stock of eels >150 mm was estimated to be 129 076 (74 022–200 206) individuals (see Table 3 for details). Based on equation (3), the total mortality rates in protected and fished areas, and the stock assessment of eel under full exploitation, we estimated that the total harvest by fishermen accounted for 10630 eels (5231–16994). Based on the proportion of silver eels calculated in fished and protected areas, we estimated the silver eels production to be 1961 (1431–2000) ind·year^{-1}, with a mean production of 11.3 and 3.1 silver eel·ha^{-1} in the protected and fished areas, respectively. Thus, the mean production of silver eels in a protected area would be 3.6 times higher than in the fished area. The production of the protected areas, that cover 2.4% of the total aquatic area (596.6 ha), would represent 8.4% (±0.43 SE) of the silver eel biomass produced in the whole study area. We estimated that a fully protected GBM would produce 6742 silver eels (596.6 ha × 11.3 eel·ha^{-1}). The GBM is currently estimated to produce 1961 silver eels, thus the fishery activity currently is estimated to remove approximately 71% of the silver eel production of a fully protected GBM. Then, it is possible to estimate the surface of marshes to be protected, in accordance with a management objective. For example, 50% of the potential eel biomass of a fully protected GBM would represent

Table 3. Parameters (number, density and biomass) of eel stock and silver eel production assessed at each zone of the Grande Brière Mottière marsh. Values in parenthesis represent the minimum and maximum estimations. See text for details on the calculation.

			Eel population			Silver eel production		
Zone	Status	Aquatic habitat (ha)	Number of individuals	Density (ind·ha^{-1})	Biomass (kg·ha^{-1})	Number of individuals	Density (ind·ha^{-1})	Biomass (kg·ha^{-1})
1	Fished	69.7	11450 (6201; 20205)	164.2 (88.9; 289.7)	11.84 (5.58; 23.58)	163 (88; 287)	2.3 (1.3; 4.1)	1.34 (0.75; 2.39)
2	Fished	160.7	30875 (18266; 35271)	192.1 (113.7; 219.5)	8.67 (4.86; 10.45)	438 (259; 501)	2.7 (1.6; 3.1)	1.57 (0.93; 1.81)
3	Fished	12.9	2610 (1205; 6125)	202.0 (93.3; 474.1)	10.05 (4.21; 25.75)	37 (17; 87)	2.9 (1.3; 6.7)	1.69 (0.75; 3.91)
4	Fished	25.7	14832 (8825; 30113)	577.0 (343.3; 1171.6)	37.62 (20.44; 83.00)	211 (125; 428)	8.2 (4.9; 16.7)	4.79 (2.86; 9.75)
5	Fished	112.0	24230 (15317; 36474)	216.3 (136.7; 325.6)	10.42 (5.96; 17.17)	344 (218; 518)	3.1 (1.9; 4.6)	1.81 (1.11; 2.68)
6	Fished	78.3	23076 (12816; 40970)	294.7 (163.7; 523.2)	24.07 (12.34; 46.00)	328 (182; 582)	4.2 (2.3; 7.4)	2.45 (1.34; 4.32)
7	Fished	39.8	9527 (5282; 14489)	239.5 (132.8; 364.2)	13.60 (7.13; 21.81)	135 (75; 206)	3.4 (1.9; 5.2)	1.98 (1.11; 3.03)
8	Fished	82.9	9894 (4574; 13112)	119.4 (55.2; 158.2)	8.43 (3.29; 12.89)	140 (65; 186)	1.7 (0.8; 2.2)	0.99 (0.46; 1.28)
9	Protected	6.5	614 (419; 703)	94.1 (64.2; 107.8)	5.85 (3.49; 7.55)	39 (27; 45)	6.0 (4.1; 6.9)	3.50 (2.39; 4.03)
10	Protected	8.1	1968 (1117; 2744)	242.8 (137.8; 338.5)	23.24 (10.94; 37.91)	126 (71; 175)	15.5 (8.8; 21.6)	9.05 (5.14; 12.6)

3371 silver eels. Considering that the protected area would always have a mean production of silver eels 3.6 times higher than those in the fished area (i.e., 11.3 and 3.1 silver eels·ha^{-1}, respectively), 3371 silver eels could be produced with 31.1% of the GBM protected. Indeed, 31.1% of protected area (185.5 ha) would produce 2096 silver eels and 411.1 ha of fished areas would produce 1275 silver eels. Consequently, only 31.1% (185.5 ha) of protected aquatic habitat of the GBM would produce, with the unprotected area, 50% of the potential eel biomass of a fully protected GBM.

Discussion

Freshwater protected areas: a compromise between eel global management and local fishery activities

The analysis of catch data and scientific surveys in the GBM freshwater marshes between 2004 and 2005 provided evidence for the efficiency of a protection policy for guaranteeing a local production of silver eels and maintaining a traditional fishery activity. Indeed, the protected area showed a mean production of silver eel (ind·ha^{-1}) around 3.6 times more than the fished areas and 2.4% (14.6 ha) of protected area in the GBM produces 8.4% of the current silver eel production (in biomass). Consequently, a size adjustment of the protected areas to 31.1% (185.5 ha of aquatic habitat) with maintaining the current fishery in the remaining parts might produce 50% of the potential eel biomass of a fully protected GBM. This could be a management target usable by local managers. Nevertheless, the optimal size of protected areas is difficult to estimate because the consequences of the protected areas extension have never been thoroughly investigated to establish valid rules for the design of freshwater protected areas (size, connectivity, location, land covered, etc.), or the creation of new habitats (ditches) in the existing protected area. Another crucial point is that we do not know the proportion of individuals that escape from the silver eel fishery when they migrate seaward and reach safely the spawning area as well as the level of eel movements between protected and fished areas within the marsh.

The conservation of freshwater fish and fisheries is the greatest challenge facing the sustainable development of inland waters (Arlinghaus et al. 2002). Inland fisheries are of high economic and socio-cultural importance, providing a ‘myriad of benefits to society’ (Arlinghaus et al. 2002; Cowx & Gerdeaux 2004). By far, the most dominant traditional inland fisheries management practises in Europe are regulations and stocking. To a lesser extent, inland fisheries management uses habitat restoration to increase the potential production of the fishery (see review in Arlinghaus et al. 2002). The use of freshwater protected areas to manage eel populations is in keeping with the last aspect. Because the management of the wide panmictic European eel population is particularly complex (such a challenge has never happened before), it faces some highly variable socio-economic and legislation constraints. Therefore, case-adapted management options with respect to usages, properties and histories must be considered to significantly increase silver eel production. The use of local freshwater protected areas appears to be a relevant way to reconcile these aspects and to respond to both global management constraints and local fisheries subsistence.

Contribution of small coastal marshes to the European eel population

Small coastal marshes contribute to the overall growth, and the reproduction of the European eel population by precise quantification remains impossible. In the present study, we estimated that a single marsh on the European Atlantic coast (GBM 7000 ha total area) supports a sub-population of about 130 000 eels and potentially produces about 1961 silver eels·year^{-1}, almost exclusively composed of females. Coastal marshes cover 230 000 ha of land on the western French coast (Feunteun et al. 1992). Given our findings in the present study, it can be assumed that these ecosystems produce a significant number of female silver eels. Moreover, eels produced in coastal marshes are exposed to fewer hazards than those in rivers because such marshes are not equipped with hydroelectric stations, that damage or kill 20–100% of the silver migrants passing through their turbines (Travade & Larinier 1992; McCleave 2001; Gibson & Myers 2002). In addition, these coastal marshes are small, only connected to the sea, and they are a part of nonintensive agricultural landscapes. Together, these factors probably account for the quality of the silver eel production. It is especially interesting to consider that coastal marshes’ characteristics can influence the sex ratio. In places where the eel abundance, is about 100–150 kg·ha^{-1} (110–170 kg·ha^{-1} on the Frémur River, Acou et al. 2007; 90–159 kg·ha^{-1} on the Rio Esva, Lobon-Cervìa et al. 1995), silver eels are mainly males (94.7% and >99% for the Frémur River and the Rio Esva, respectively), whereas when the eel abundance is relatively low (3.5 kg·ha^{-1} on the Imsa River, Vøllestad & Jonsson 1988; 35–45 kg·ha^{-1} on the Oir River, Acou et al. 2007), silver eels are mainly females (>90% and around 80% for the Imsa and Oir Rivers, respectively). Thus, the observed over-dominance of females in the GBM and the low abundance of yellow eels (15.4 kg·ha^{-1}, see Table 3) are consistent with observations from other areas with low abundance where females are the numerically dominant sex. On the other hand, the proportion of silver eels observed in the GBM is comparable with those reported in other systems at the same latitude (6.0% and 12.6% in Oir and Fremur rivers, respectively, Acou et al. 2005; 8.7% and 8.9% in the Fremur river, Feunteun et al. 2000; 5.9%, 1.3% and 5.8% in the Fremur river in 2000, 2001 and 2002, respectively, Acou et al., in press). As Vøllestad (1990) recommended retaining yellow-eel fishery activity to maximise the silver eel fishery landings, it seems likely that, by limiting the yellow eel abundance in the GBM to <50 kg·ha^{-1}, the traditional fishery might contribute to the local production of large silver eels. This might be influenced by a low recruitment that leads to a low elver eel abundance, and by the high food availability because of the recent introduction of the invasive red swamp crayfish (*Procambarus clarkii*) that can be preyed by eels (Domingos et al. 2006).

Such prospects are crucial from a conservation viewpoint, as one of the main recommendations of international managers (EELREP 2005; ICES WGEEL 2006) is to protect aquatic systems with a high proportion of large healthy silver eels. In the present study, we quantified fishing practices and evaluated their influence on the local eel population. Such issues are important, as the identification of mortality causes and their quantification are difficult in the wild but are keys for international eel management (Feunteun et al. 2000; Feunteun 2002). The presence of protected areas allowed us to determine the mean natural mortality was relatively low in the marsh (12%·year^{-1}) and comparable with those observed in other ecosystems for the same life stages (Adam 1997; Feunteun et al. 2000). Nevertheless, our estimation of fishermen's captures based on biological data, [i.e., 10 630 individuals (5231–16 994)], was somewhat lower than that resulting from questionnaires [i.e., 23 882 individuals (18 206–29 578)]. This might arise because fishermen had difficulties to evaluate their catches accurately, underlining the importance of logbooks to conduct fishery surveys.

Establishment of freshwater protected area

Freshwater protected areas have already been shown to be efficient for conserving bird and fish diversity (Eybert et al. 1998; Keith 2000; Self 2005) and their adaptation for the local eel population management could be included in the overall management of freshwater biodiversity (Noble et al. 2004). Recent research in marine protected areas has demonstrated that fish populations benefit from protected areas not just for the overexploited poorly mobile species, but also (to a lesser extent) for under-exploited stocks and highly mobile species (Apostolaki et al. 2002). Thus, the creation of freshwater protected areas might also benefit vulnerable or endangered freshwater fish species, such as has already been advocated for the Northern pike, *Esox lucius* (Rosell & MacOscar 2002).

The efficiency of protected areas in other inland ecosystems remains to be assessed. Concerning estuarine and coastal waters, Naismith & Knights (1990a,b) indicated that commercial fishery in the Thames estuary was having minimal impact on the eel stock, and fishing mortality was masked by natural mortality and migration effects. In the same way, in the Hudson River estuary, Morrison & Secor (2003) suggested that brackish-water areas could support a higher fishing mortality than freshwater areas. Such analyses confirm that protected areas for eels might not be relevantly usable in open habitats like estuaries or coastal areas, and that this management tool might be preferentially applied into confined freshwater areas, such as coastal marshes (Morrison & Secor 2003). Furthermore, the restricted yellow eel home range in several types of freshwater ecosystems (Baras et al. 1998; Jellyman & Sykes 2003; Laffaille et al. 2005b) offers opportunity for a wider application of this measure.

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