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Factors affecting otter (*Lutra lutra*) abundance and breeding success in freshwater habitats of the northeastern Iberian Peninsula

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Abstract Otters are elusive semi-aquatic mammals, occurring in low densities and difficult to count. A study was conducted in 15 stretches (10–12 km) of four tributaries of the Ebro River, with the aims to understand spatial and temporal changes in otter abundance and breeding success and the causes of such variations. Between 1990 and 2009, both otter parameters were assessed by means of visual spring–early summer censuses, carried out by sets of observers located every 500 m. A total of 134 censuses were carried out, involving 4,540 twilight watches (7,896.5 h) and 520 otter sightings were recorded. Also, 39 different habitat characteristics (including prey species) were established for each stretch. Otter abundance was assessed by means of three indexes related to the census effort and the length and surface units (in terms of otter habitat). Excluding the upper stretches, we found on average 0.07–0.26 adult and subadults per kilometre (1.45–6.26/km²). Important interannual fluctuations in otter abundance and breeding success were found in some Pyrenean stretches located downstream of a large reservoir. This was linked to the effect of autumn floods (in part due to the opening of dams) on the fish stocks (mainly Barbels).

Similar habitat conditions resulted in similar abundances between stretches, and different habitat conditions generated different abundances in adjacent stretches of the same river. No significant differences were found for litter size between small cubs (1.60±0.70 cubs per litter) and large cubs (1.39±0.50) as a whole, but differences between stretches were found. On average we found between 0.009 and 0.130 large cubs per year per kilometre. Otters bred more successfully in stretches with higher otter densities. Otter abundance and breeding success correlated negatively with altitude as a consequence of the interaction of several habitat characteristics with altitude. The stepwise linear regression linked the number of adult otters per kilometre with the ecosystem production (chlorophyll *a* concentration), while the number of large cubs per kilometre per year was linked with the food (fish+crayfish) abundance. The findings bring about a consistent and congruent scenario of otter abundance and breeding success explained by the different steps along the food chain.

Keywords Otter · *Lutra lutra* · Abundance · Breeding · Density

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Introduction

The Eurasian otter, *Lutra lutra*, is an elusive semi-aquatic mammal, mostly crepuscular and occurring in low densities (Mason and Macdonald 1986; Kruuk 2006). Except in some coastal sea habitats of northern Europe, the otter is often difficult to observe and, therefore, to count. These are the main reasons for the scarce amount of literature concerning Eurasian otter abundances and densities (Chanin 2003). There is a considerable heterogeneity in the census methods

conducted, abundance indices used, classes (age class, sex, behavioural condition) and habitats considered (Kalz et al. 2006). In terms of reproduction, the Eurasian otter is a facultative polyoestrous species that produces small litters ranging on average from 1 to 2.5 cubs per female (Chanin 2003).

The Eurasian otter feeds predominantly on aquatic and semi-aquatic prey (Mason and Macdonald 1986; Ruiz-Olmo and Palazón 1997) and is considered a food-limited species (Kruuk and Carss 1996). Being a Mustelid—a family with a higher basal metabolism than other Carnivore groups—with a semi-aquatic way of life, it has a higher energy demand compared with other terrestrial carnivore species with similar body mass (Iversen 1972; Gittlemann and Oftedal 1987; McNaab 1989; Oftedal and Gittleman 1989). This increased energy demand constitutes a constraint on population size and reproductive success (Kruuk et al. 1987). For this reason, some authors have proposed that otter abundance and breeding success are mainly affected by resource availability (Kruuk et al. 1987, 1993; Sidorovich 1997; Ruiz-Olmo et al. 2001a), and it has been reported that changes or fluctuations in otter breeding success are usually related to food availability (Kruuk 2006; Elmeros and Madsen 1999; Ruiz-Olmo et al. 2001a, 2002). These studies focused only on the effects of food. However, other factors have been suggested as variables affecting otter abundance and reproductive success: (a) habitat structure such as river or other water system size, water flow, presence of islands, riparian vegetation, stones, etc. (Mason and Macdonald 1986; Sidorovich 1997; Ruiz-Olmo and Jiménez 2008); (b) habitat stability (Ruiz-Olmo and Jiménez 2008); (c) water level changes and dynamics, including the effect of droughts, floods and periods of frost and ice cover (Sidorovich 1997; Ruiz-Olmo et al. 2002); (d) altitude (Ruiz-Olmo and Jiménez 2008); (e) availability of shelters and dens (both are usually linked to geologic basin features; Kruuk et al. 1989; Yoxon 2000); (f) presence of beaver dams and lodges (Sidorovich 1997); (g) degree of water pollution (Gutleb 2000; Sidorovich 1997); (h) competition with other fish and crayfish/crab-eating species (Kruuk 2006); (i) spatial behaviour (Kruuk 2006; Ruiz-Olmo et al. 2001a; Jiménez 2005) and (j) hunting and other human impacts (Sidorovich 1997). Any of these factors may affect population dynamics, either directly or indirectly through changes in food availability.

Unfortunately, otter counting methods are not yet sufficiently standardised (Chanin 2003), thus yielding inconsistent or misleading results. As an example, counting estimations are often given as total number of otters in one population, but not considering age class (adults, subadults, cubs), spatial use class (sedentary, dispersals, transients) and others. But simple numbers do not allow the estimation of population sustainability. Thus, an effort

in methodology standardisation and term definition is required.

Estimations of abundance or breeding success are usually given for short periods of time not taking into account fluctuations in population size and breeding parameters, as shown by the few long-term studies on otter numbers and breeding success (Kruuk 2006; Sidorovich 2000; Ruiz-Olmo et al. 2001a). Thus, there is a lack in both standardised counting methodologies and long-term works. The present study focuses on both topics. Our aims were (a) to measure how otter abundance and reproductive parameters fluctuated over a long period, (b) to determine the causes of these fluctuations and (c) to develop predictive models for otter abundance and breeding success in the Iberian freshwater ecosystems. We paid particular attention to the possible effects of physical or chemical water characteristics, water flow and dynamics, climatic variables, habitat structure, ecosystem stability, ecosystem productivity and production, fish and crayfish abundance and altitude.

Methods

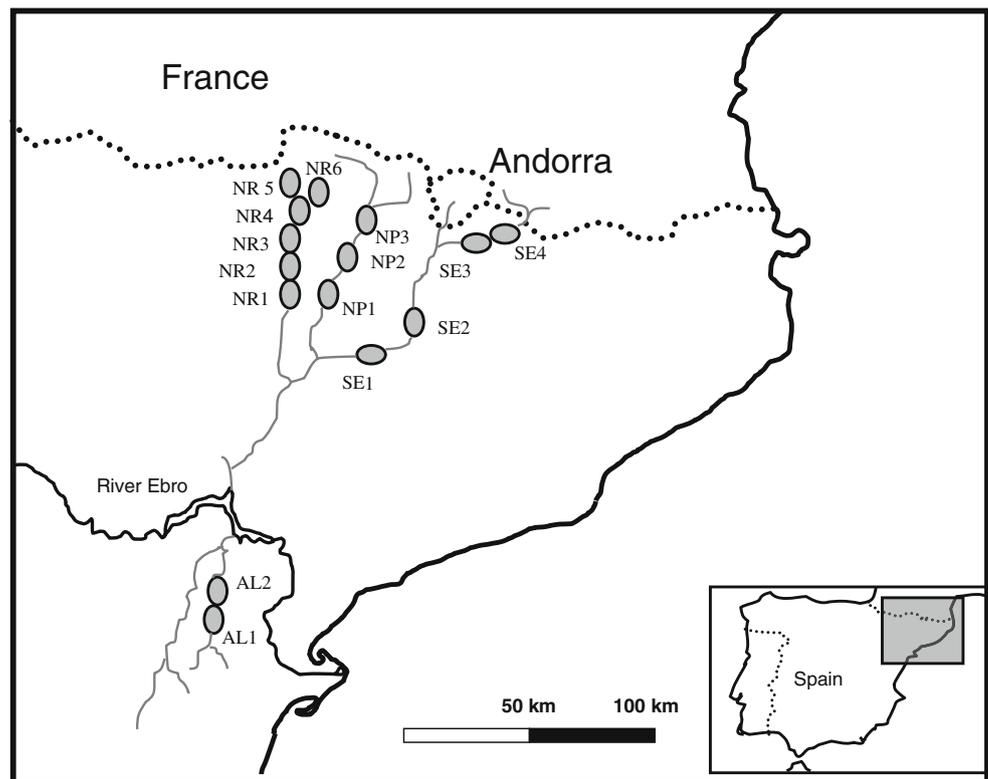
Study area

The study was conducted in several tributaries of the Ebro River located in the northeast of the Iberian Peninsula in Spain (Fig. 1). The sample area comprises the most important and widespread types of physiographical ecozones occurring within the Ebro Basin, including the gradients in between (Ruiz-Olmo and Jiménez 2008; Table 1). A total of 15 stretches of the rivers Noguera Ribagorçana (six stretches; NR1–NR6), Noguera Pallaresa (three; NP1–NP3), Segre (four; SE1–SE4) and Algars (two; AL1 and AL2) were surveyed. The stretches NR1, NR2 and NP1–NP3 were selected as a representation of the only rivers having otter populations in 1990. The remaining stretches were added progressively as the otters recovered.

Visual censuses

Otter abundance was assessed by means of visual censuses (direct counts), carried out between May 15 and July 15 during the years 1990 to 2009. In the study area, otters show higher rates of activity during twilight periods. Based upon this fact, we developed a standardised method (Ruiz-Olmo 1993; Ruiz-Olmo et al. 2001b) that involves a set of observers positioned at regular distances along riverbanks, taking note of every otter movement in order to record the minimum number of individuals per stretch. Average distance between observers was 500 m, with observers choosing an optimal viewing point within a range of 100 m from these distance points. Sighting reports included time, location of individuals, direction of

Fig. 1 Study area showing the monitored stretches



movements, group size, relative individual size and behaviour (i.e. cubs with mother, play, mating). We defined:

- *Vigil*: Otter count carried out by a single observer at a previously fixed viewpoint of the river bank. Viewpoints were chosen to allow a clear view over a minimum length of both sides of the bank. Morning and evening vigils carried out at the same point were considered as different. Vigils were carried out at dusk from 6 p.m. to 8:15 p.m. (GMT) and at dawn from 3:30 a.m. to 5 a.m. (GMT).
- *Observation*: The visual detection of one otter during a vigil. If an otter was observed almost permanently, it was considered to be the same observation and only counted once. But when an otter was sighted 15 min (or more) after a previously observed otter had gone out of sight and no evidence existed of the otter being the same, then this *observation* was considered to be a different *one*. When more than one otter was seen simultaneously, each individual was noted as separate otter *observations*.
- *Census*: An operation using sets of observers along 10–12 km of a river carrying out vigils, in order to count the minimum number of otters present in the surveyed stretch during a given period of time. A census included the vigils carried out at consecutive dusks and dawns. Thus, a census comprised the otter activity, recorded per day.

How to assure that all otters present are also scored?

Censuses are affected by different kinds of biases. An obvious question that arises from the methodology is whether all otters present in a stretch are recorded by the census. Counting elusive animals always bears the risk of missing some of the individuals during a count. Thus, we must ask: (a) is the method suitable to assess otter abundance and their spatial and temporal variations? and (b) will our data be a good estimate of actual densities?

In a previous study, we tracked and analysed the activity patterns of radio-tracked otters in northeast Iberia and surrounding areas (Ruiz-Olmo et al. 2001b). Comparing this data set with the ones from censuses conducted simultaneously revealed that almost all individuals were active outside the dens (visible) during or around twilight hours. We therefore concluded that direct counts at these hours will provide good estimates of otter population densities.

Other factors that could also affect the outcome are (a) low visibility at counting spots, (b) observers with lack of proper experience and (c) disturbance (Ruiz-Olmo 1993). In order to minimise these potential bias sources, we maximised the number of experienced observers, always chose viewing spots with high visibility over the river bank sections and conducted the surveys in areas without any

Table 1 (continued)

	Noguera Pallaresa			Segre		Algars			
	NP 2	NP 3	SE 1	SE2	SE 3	SE 4	AL 1	AL2	
Total visual censuses ^c	2	4	4	3	9	9	22	2	
Total vigils carried out	72	86	101	84	434	444	708	80	
Total vigils time (h)	137.3	133.5	159.7	152.3	658.2	725.5	1,277.9	144.1	
Total observations of otters	4	0	6	6	22	33	136	9	

Species (crayfish in bold letters, fish in italic, amphibian underlined and Reptile in bold and underlined)

^a Main species in diet included species accounting for more than 5%

^b Visual censuses

^c Each census including dusk and sunset vigils during the same otter activity period including all the censuses carried out during all the years surveyed

known external factor that could have become a source of disturbance to otter behaviour.

How to assure that stretches are long enough?

To assess the minimum length, a large operation was carried out in a 30-km section of the river Noguera Ribagorçana, involving 60 observers at vigil points. Two censuses on consecutive days were conducted in 2002 between the 5th and 7th of June (240 vigils total). The number of otters observed and their positions were considered for all combinations of stretches of different lengths between 1 and 25 km. We estimated mean density, standard deviation, variance and error for each stretch length.

Adults, cubs, residents and dispersal

Estimates of otter abundances and densities are usually given as the total number of otters detected in a stretch of a river or a shoreline (Erlinge 1968). This is due to the fact that otters are difficult to study and therefore surveys are often carried out by means of indirect methods. The inclusion of cubs in such estimates may be misleading as data on mammal abundances are commonly presented in terms of adults, adult-sized individuals or breeders. For this reason, we developed indexes excluding the cubs. The results on cubs were included in the breeding sections.

Another concern is whether or not ‘non-breeders’ (subadults) or ‘non-residents’ (‘transients’, ‘floaters’, ‘dispersers’) should be considered in the counts or estimates. These otters are almost the same size, have similar nutritional needs and spend some of their time in the study area, and thus, it is often not possible to distinguish these classes during the visual censuses. Finally, no consistent definitions of ‘non-residents’ are found within the literature (see, for example, Hung et al. 2004). We also must consider that home ranges vary among individuals and throughout an individual’s life and may become very small rendering detection of otters very difficult. This applies, for example, to breeding females, to large cubs before dispersal or even to most of the population when resource levels are high but only available in small rich patches (Kruuk 2006; Saavedra 2002; Ruiz-Olmo et al. 2005). Such biases could be caused by collecting too few spraints or tracks in sampling grids, or by low sample intensity studies which may mistakenly consider individuals as transients or floaters because they were detected only one or a few times. We included ‘dispersers’ in the calculations as the most accepted definition (Kruuk 2006), leading to an index in which adult-sized otters refer to adults and dispersing otters combined (*AddOtters*).

Indexes of otter abundance, density and breeding success

We used the following as estimators of otter abundance:

- Probability to observe an adult and/or a dispersing otter during a vigil (= observations of adult and dispersing otters/vigil carried out; *AdDOtter/vigil*). This is an estimation of the otters detected in terms of effort.
- Number of different adult and dispersing otters observed per kilometre (*AdDOtter/km*). This is an estimation of the otters detected per unit length.
- Number of different adult and dispersing otters observed per square kilometre (*AdDOtter/km²*). This is an estimation of the otters detected per surface units. This index was used in an inverse manner by Kruuk (2006), as surface of otter habitat (hectares) per otter. This index was measured in relation to otter habitat extent rather than to water width or surface. For general purposes, we established the mean otter habitat width using measurements taken every 250 m along the river axis for the studied stretch. Available data from both radio-tracked and tracked otters (Ruiz-Olmo et al. 2001b; Jiménez 2005) and visual monitoring in the studied river sections were used to estimate the extent of otter habitat. Because otters move not only within the water but also in other riparian habitats, we included the border between riparian and non-riparian habitats. When the drawn boundaries of the riparian habitats were surpassed by real movements, we used those. Thus, surface was calculated as the product of the stretch length and the mean riparian habitat+mean water width.

Complementary track censuses

In our study area, we have previously found consistent agreement between densities estimated through direct counts and those from track counts when only new footprints were considered (1 to 2 days old; Ruiz-Olmo et al. 2001b). Thus, for periods prior to the development of the visual census methodology (1985 to 1987), we included track data in the analysis to assess otter density fluctuations in stretches NR1 and NR2. For stretch NP1, we did this in 2002 and 2003 as well, when no direct counts had been taken for logistic reasons.

Breeding success

A supplementary benefit of the visual census method is that otter litters are easily observed and that their size and age class can be easily and accurately established while observing the individuals. According to Ruiz-Olmo et al. (2002), we classified litters as: *small cub litters* (cubs 2 to 6 months old; total length (TL)<90% of their mother's TL)

and *large cubs litters* (cubs older than 6 months; TL>90% of their mother's TL).

Characteristics of the studied habitat

We selected and defined a number of variables (Table 2). All values for these variables were estimated based upon data specifically collected in the river sections surveyed, except for those marked by <+> in Table 2, which represent mean values of data collected by the Catalanian Water Agency sampling stations network (<http://aca-web.gencat.cat/aca>). The lack of data for the variable 'plant biomass production' (CHLOROPH) for a few stretches was overcome by using the correlation found between chlorophyll a concentration and water conductivity at all sampling points within the Ebro Basin: CHLOROPH=0.0085 COND+0.3767; R=0.897; P<0.0001, allowing the calculation of CHLOROPH values.

For stretch NR1, we assessed fish biomass abundance (grams per square metre) because on average fish make up >95% of prey (Ruiz-Olmo et al. 2001a, b). Reasons for selecting NR1 were (a) structural and general attributes were more or less constant across years, (b) fishing is forbidden, thus reducing human impact, and (c) no direct human-caused fish mortality had been recorded over the 20-year monitoring period. We determined Ebro's Barbel (*Barbus graellsii*) and Ebro's Nase (*Chondrostoma miegii*) to be the dominant species in terms of biomass levels. In low numbers, we also found *Salmo trutta*, *Leuciscus cephalus*, *Cyprinus carpio*, *Alburnus alburnus* and *Micropterus salmoides*.

We assumed the main effects on otter abundances to be water-caused perturbations. For this, we used river flow data gathered by the Spanish continental water management services (Confederación Hidrográfica del Ebro) from sampling station E115 *El Pont de Montañana*, which lies within the study area. In particular we used (a) total amount of water (million cubic metres) flowing through the stretch in the spring (April to June), which is an estimate of the potential temporary effect of flow and floods on fish at the time of upstream movements (Ruiz-Olmo et al. 2002); (b) total amount water (million cubic metres) that flowed through the stretch during the previous 12 months and (c) total amount of water (million cubic metres) that flowed through the stretch during the autumn (September to November) previous to the considered census date, this being the season with heavier rainfalls and heavy floods.

Statistics

Means, standard deviations and errors were calculated according to Fowler and Cohen (1999). As samples were not normally distributed, mean litter size results were compared using the Mann–Whitney *U* test (Fowler and Cohen 1999). In order to compare the range of fluctuations

Table 2 Habitat characteristics studied for each stretch

Category of habitat characteristic	Description	Name	Score
Chemical and physical water characteristics	Ammonium ion concentration in mg/l ^a	NH ₃ ⁺	
	Water conductivity at 20°C in µS/cm ^a	COND	
	Phosphates (P ₂ O ₅ ⁻) concentration in mg/l ^a	PHOSP	
	Nitrite ion concentration in mg/l ^a	NO ₂ ⁻	
	Sulphate ion (SO ₄ ²⁻) concentration in mg/l ^a	SULPH	
	Dissolved oxygen in mg/l ^a	O ₂ ⁻	
	Percentage of oxygen saturation ^a	%O	
Water dynamics	Water temperature in °C ^a	WATEM	
	Average depth in m	DEPTH	
	Water persistence	WATER	0: dry riverbed, 1: several small ponds present, 2: many ponds present, 3: continuous shallow water, 4: continuous abundant water with some scarce ponds and 5: continuous water and many ponds
	Average flow	FLOW	1, 0–0.1 m ³ /s; 2, 0.1–0.5 m ³ /s; 3, 0.5–2.0 m ³ /s; 4, 2.0–10 m ³ /s and 5, >10 m ³ /s
	Flow type	FLTYP	1: rough waters forming small waterfalls or cascades, 2: rough waters only, 3: calm and rough waters combined, 4: still waters (with a very slow movement) and 5: static waters
Circannual weather variables	Mean of monthly minimum temperatures in °C	TMIN	
	Mean of monthly maximum temperatures in °C	TMAX	
	Mean of monthly precipitation in mm	RAIN	
Habitat structure	Mean width of the water in m	SWIDT	
	Otter habitat width in m	WIDTH	
	Presence of ponds deeper than 1 m	PONDS	0 when none, 1 when on average <0.5 ponds/km, 2 when 0.5–1 ponds/km, 3 when 1.1–2 ponds/km, 4 when 2.1–5 ponds/km and 5 when >5 ponds/km
	Presence of islands or river branches	ISLBR	0: none present, 1: minimal presence, typically only one, 2: only a few, 3: common along the section, covering more or less half of the length of the stretch, 4: very common (along most of the section) and 5: present along the entire stretch; riverbank vegetation cover (trees and bushes)
	Riverbank vegetation cover (trees and bushes)	VEGET	(1)
	Riverbank helophytic vegetation cover	HELOP	(1)
	Abundance of rocky systems (2)	ROCKY	(2)
Presence of tributary junctions (2)	JUNCT	(2)	
Altitude	Altitude above sea level in m	ALTIT	
Ecosystem stability	Presence/absence of the tail or rear part of a big reservoir within the studied stretch	RTAIL	1 (presence) or 0 (absence)
	Presence/absence of a big reservoir upstream	BIGUP	1 (presence) or 0 (absence)
	Presence/absence of a big reservoir downstream	BDOWN	1 (presence) or 0 (absence)
	Habitat stability	STABIL	= WATER+FLOW+FLTYPE
Plant biomass production	Concentration of chlorophyll a in mg/l ^a	CHLOROPH	
Food diversity and fish and crayfish abundance	Number of main food species	SP>5%	Those with a relative frequency in diet >5%
	Fish abundance	FISH	0 (0 g/m ²), 1 (0.01–1.0 g/m ²), 2 (1.0–13.0 g/m ²), 3 (13.0–20.0 g/m ²), 4 (20.0–48.0 g/m ²) and 5 (over 48.0 g/m ²)
	Crayfish abundance	CRFISH	0 (0 seen on the stretch), 1 (1 seen), 2 (2 to 20 seen g/m ²), 3 (frequent observation and difficult to quantify), 4 (abundant) and 5 (extremely abundant)
	Total fish and crayfish abundance	FOOD	= FISH+CRFISH

^a Values were 0, none; 1, <0.5 junctions or rock systems/km; 2, 0.5–1.0/km; 3, 1.1–2/km; 4, 2.1–5/km and 5, >5/km

^b Values were 0, absent; 1, 1–20%; 2, 21–40%; 3, 41–60%; 4, 61–80% and 5, >80%

in otter abundance between stretches through the years, the median absolute deviation (MAD) of AdDOtter/km for each year was used (Venables and Ripley, 1999). It is a measure of the variability of a univariate sample of quantitative data. Univariate analysis was done by means of correlation. Autocorrelation was tested by means of the Durbin and Watson (1951) test.

For further analysis, in order to homogenise variables, a logarithmic, arcsin or square root transformation was determined for variables requiring it (Zar 1984; Fowler and Cohen 1999). Then, a multivariate approach by means of principal component analysis (PCA; Digby and Kempton 1987) was used to analyse both otter abundance indexes and the breeding success index as dependent and the rest of the habitat characteristics. The aim of this was to reduce variables (excluding redundant ones in the subsequent analyses) and to assess main patterns. To fix the number of principal components or factors involved in the analysis, we used the Kaiser–Guttman method (Guttman 1954; Kaiser 1960). Also, to get the predictive models for dependent factors, we used a stepwise multiple regression. To avoid effect of the autocorrelation, a subsequent test for residuals to be autocorrelated using the Durbin and Watson (1951) test was performed.

Results

Visual census stretch length

Considering the experiment carried out in river Noguera Ribagorçana during the censuses conducted in June 2002, a total of 30 otter observations were made from eight different otters in a river segment of 30 km. As a whole, density is estimated to be 0.4 otters per kilometre (without considering otter class). However, these results varied greatly according to the different lengths of stretches considered (Fig. 2). The mean otter per kilometre estimations per census sector length ranged from 0.30 to 0.55 otters per kilometre, with extreme values ranging from 0 to 3.0. The maximum values estimated for mean density, standard deviation, variance and error occurred when the shorter census stretch lengths were considered. An asymptotic value was found at stretch lengths of about 10 km. According to these results, the length of stretches used in this study for visual censuses normally ranged from ten to 12 km.

Effort, otters observed and absence of influence of weather and moon phase on the results

Between 1990 and 2009, a total of 134 visual censuses were carried out in the 15 river stretches studied (Table 1).

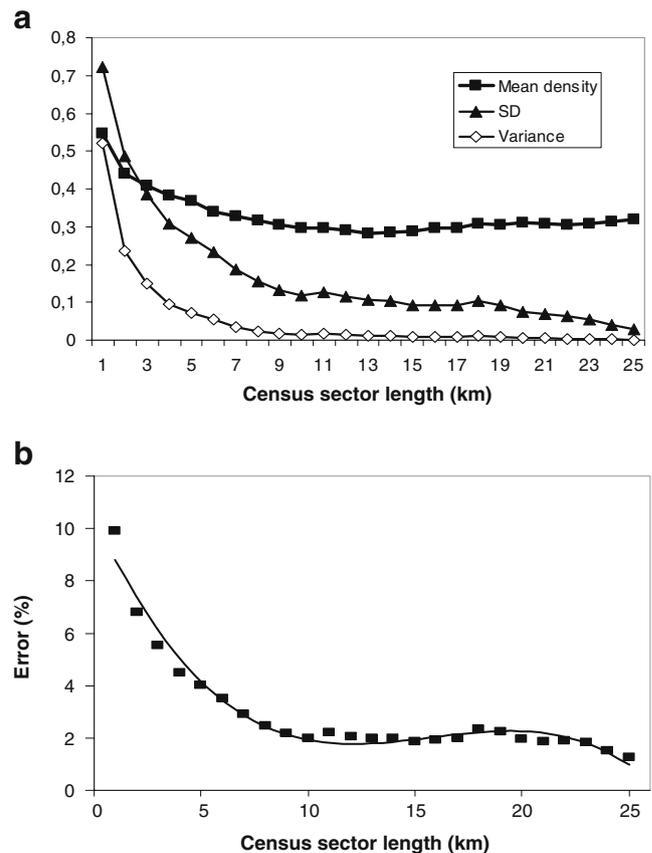


Fig. 2 Assessment of the minimum stretch length for the visual otter censuses in the river Noguera Ribagorçana, in a 30-km section, using the method described in this paper based on sets of observers placed every 500 m (June 5 to 7, 2002). **a** Mean density, SD and variance; **b** error

They involved 4,540 vigils that made up 7,896.5 waiting hours on rivers banks. A vigil lasted on average only 1.74 h, which was less than the expected 1.875 h. This was due to several causes such as weather changes, difficulties in reaching the bank among others. During these periods, we recorded 520 otter sightings over a total of 31 h and 45 min. After rejecting reiterative sights of the same otter—made by both the same or different observers—197 different otters were located during the visual censuses, of which 152 were adult-sized otters (adults and dispersers) and 45 were cubs (34 large cubs and 11 small ones). Each otter was observed by a mean number of 1.98 ± 2.02 observers during a census, the mean between stretches ranging from 1.00 to 8.00. Thus, each otter had an average probability of being observed at least twice during a single census.

No significant effect of the stretch length on otter density was observed when considering the latter as AdDOtter/km ($r=0.283$; $P>0.05$). This also applied to the relation between otter densities and average stretch width, a measure of the extent of habitat being observed from vigil points (AdDOtter/km: $r=0.100$; $P>0.05$), and to the

number of vigils carried out during censuses (AdDOtter/km: $r=0.105, P>0.05$).

For NR1 (with a monitoring period of 20 years), we could assess the effect of the climatic conditions and the phase of the moon on the otter abundance estimations. No significant effect on AdDOtter/km was found for wind intensity ($r=0.171; P>0.05$), the presence of rain ($r=0.165; P>0.05$) or clouds ($r=0.284; P>0.05$), the phase of the moon ($r=0.254; P>0.05$) or the amount of moonlight ($r=0.384; P>0.05$).

Results on otter abundance from visual censuses

The functions fitted in order to assess otter abundance in the study area by means of the different indexes were:

$$\text{AdDOtter/vigil} = 0.79 \text{ AdDOtter/km} - 13.25$$

$$r^2 = 0.659, P < 0.00001$$

$$\text{AdDOtter/km}^2 = 16.58 \text{ AdDOtter/km} + 0.3518$$

$$r^2 = 0.762, P < 0.00001$$

When considering all average data from the 15 surveyed stretches as one sample, we obtained on average 0.125 ± 0.14 AdDOtter/vigil (mean \pm SD; range 0–0.54; Table 3) or 4.2 ± 3.3 observations/100 h (0–11.07). Average abundance was 0–0.25 AdDOtter/km with a mean of 0.14 ± 0.19 . Also, an average density of 2.63 ± 1.94 AdDOtter/km² (0–6.26) was obtained (29.53 ± 21.2 ha/AdDOtter; range 0–69.04).

Spatial and temporal variations in otter densities

There were large differences in AdDOtter/km values among stretches (Table 3). While in some, mean otter abundance (AdDOtter/km) was 0 or close to 0 (NR5, NR6, NP3), in others it was higher—0.26 AdDOtter/km for NP1, 0.25 for AL2, 0.24 for AL1 and NR1 and 0.22 for SE2, which corresponds to an average of one adult-sized otter per 3.8–4.5 km of river stretch. The intermediate density values (0.07 to 0.14) corresponded to one resident adult or dispersing otter per 7.14–14.3 km.

In terms of otter habitat surface or extent, similar patterns were found. Lower values were obtained again from NR5, NR6 and NP3 (<1.0 AdDOtter/km² of suitable otter habitat), while other stretches had very high mean densities: AL1 (6.26), AL2 (5.81), NP1 (4.33) and SE4 (4.13).

In relation to temporal variations, we conducted long-term censuses on some stretches (Fig. 3). Any of the otter density series was affected by autocorrelation. Values of MAD for AdDOtter/km were low in stretches AL1 (0.16), SE3 (0.07) and SE4 (0.00), drawing a relatively constant pattern of otter abundance. However, important interannual fluctuations in adult-sized otter densities were found in NR1 (0.53), NP1 (0.43) and NR3 (0.2; showing peaks every 4 to 8 years). These stretches are located downstream of a large reservoir in the pre-Pyrenean Mountains.

We compared the latter three stretches showing larger fluctuations. No correlation was found in otter abundance

Table 3 General results of the visual censuses in each stretch and for each abundance index

River	Stretch	All the otters	Adult-sized otters	
		Different otters/vigil	AdDOtter/km	AdDOtter/km ²
Noguera Ribagorçana	NR1	0.14	0.24	3.26
	NR2	0.09	0.09	1.45
	NR3	0.04	0.07	1.94
	NR4	0.03	0.11	2.67
	NR5	0	0	0
	NR6	0	0	0
Noguera Pallaresa	NP1	0.12	0.26	4.33
	NP2	0.07	0.11	2.41
	NP3	0	0	0
Segre	SE1	0.06	0.14	1.76
	SE2	0.08	0.22	2.25
	SE3	0.05	0.17	4.13
	SE4	0.07	0.15	3.23
Algars	AL1	0.22	0.24	6.26
	AL2	0.13	0.25	5.81
Mean \pm SD		0.07 \pm 0.06	0.14 \pm 0.09	2.63 \pm 1.94

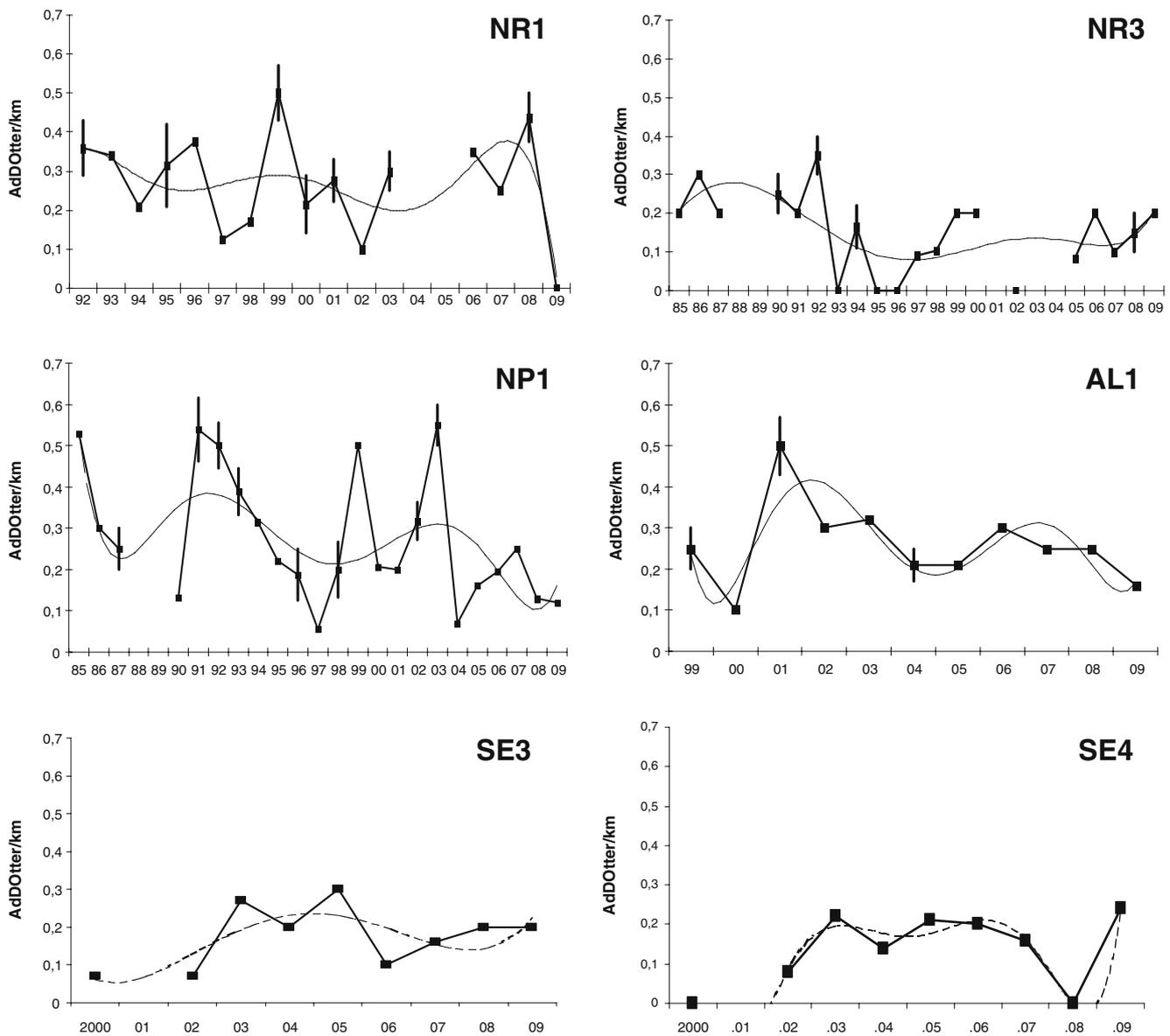


Fig. 3 Interannual fluctuations in adult and subadult (non-cub) otter abundance (AdDOtter/km) in the six stretches monitored for more than 9 years

between NR1 and NR3 (AdDOtter/km: $r=0.458$; $P>0.05$; $n=15$ years; no autocorrelation was found). Despite being in the same river and only 12 km apart, both stretches show different characteristics. However, there was a correlation throughout the years between NR1 and NP1 ($r=0.593$; $P<0.025$; $n=15$; again no autocorrelation was found). These two stretches lie at the same latitude about 16–18 km apart from each other, but have similar characteristics (for example, included the tail of a reservoir and were below another large reservoir and have the same rain and flow patterns). For similar conditions, there was a similar pattern even for unconnected rivers. For SE3 and SE4 (same river, different characteristics, 5 km away), the otter abundances were significantly different ($r=0.519$; $P>0.05$; $n=8$; no autocorrelation was

found). Thus, similar habitat conditions generated similar abundances in different rivers, and different habitat conditions generated different abundances in adjacent stretches of the same river.

Breeding success: temporal and spatial variations

For each of the 15 stretches studied, between 0% and 45.0% of the otters observed during visual censuses were cubs. Forty-one litters were observed in the six stretches surveyed for at least 9 years. Out of these, ten were small cub litters with an average of 1.60 ± 0.70 cubs per litter (mean \pm SD; range 1–3) and 31 were made up of large cubs (1.39 ± 0.50 cubs per litter, range 1–2; Tables 4 and 5). On average, large cub litters were 23% smaller (not significant considering data as a

Table 4 Results for litters observed in the studied stretches with nine or more years monitored

River			Noguera Ribagorçana		Noguera Pallaresa	Segre		Algars
Stretch			NR 1	NR 3	NP 1	SE 3	SE 4	AL 1
Years with data			20	11	13	9	9	11
Small cubs	Litter size	Mean±SD (range)	1.00±0 (1–1)	1.5±0 (1–2)	0	2.0±0 (2–2)	0	2.33±0.58 (2–3)
		N	4	2	0	1	0	3
% years with litters detected			20.0	27.3	0	11.1	0	18.2
Large cubs	Litter size	Mean±SD (range)	1.40±0.52 (1–2)	1.00±0 (1–1)	1.33±0.52 (1–2)	1.0±0 (1–1)	1.67±0.58 (1–2)	1.40±0.52 (1–2)
		N	10	1	6	1	3	10
% years with litters			40.0	9.1	38.5	11.1	33.3	90.9
Litters/year/km			0.05	0.009	0.042	0.011	0.033	0.091
Large cubs/year/km			0.070	0.009	0.062	0.011	0.055	0.127
Mortality rate (from small to large cub)			0%	33.3%	–	50.0%	–	39.1%

whole; Mann–Whitney *U* test=8.500, *df*=9, *P*=0.409). However, in some of the stretches, no cub mortality was found, while in others 30–50% of small cubs were lost.

For the following analyses, only large-sized cub litters are taken into account. Otters bred more successfully in stretches with higher otter densities (*r*=0.817; *P*=0.004).

Mean large cub litter size per stretch ranged from 1.00 large cub per litter to 1.67 across the time for which data was available (Table 4). For each of the six stretches with more than 9 years of monitoring, the mean number of large cub litters per year per kilometre varied between 0.009 and 0.091. Despite we found normally 0–1 large cub litters per

stretch, two different large cub litters occurred in NR1 in 2000 and simultaneously in NR1 and NP1 in 1992 (Table 5). Considering the large cubs, its abundance also varied between stretches, from a maximum of 0.13 large cubs per year per kilometre (AL1) to 0.009 in NR3 and 0.011 in SE3 (Table 4). While in some stretches (AL1) otters bred regularly over the years, they did not do so in others (NR3, SE3), where large cubs (usually single) were observed only in a few years. However, in stretches NR1, NP1 and SE4, large cubs were present in about half of the observation years. We located, for the six stretches, between 0.1 and 1.3 large cubs per stretch per

Table 5 Results of otter breeding (number of large cub litters and number of cubs) for each studied year estimated by means of direct counts (visual censuses), for the six stretches monitored for more than 9 years

Stretch	Year																			
	1990	91	92	93	94	95	96	97	98	99	2000	01	02	03	04	05	06	07	08	09
NR1	0 ^c /0 ^f	1/1	2/3	0/0	1/1	0/0	0/0	0/0	0/0	1/1	2/4	0/0	1/2	1/1	0/0	0/0	1/1	0/0	0/0	0/0
NR3	ns	ns	0/0	0/0	0/0	0/0	0/0	ns	ns	ns	ns	ns	0/0	0/0	0/0	1/1	0/0	0/0	0/0	0/0
NP1 ^a	ns	ns	2/3	1/1	0/0	0/0	0/0	0/0	1/1	1/1	1/2	ns	ns	ns	ns	ns	0/0	0/0	0/0	0/0
SE3 ^b	Not	Not	Not	Not	Not	ns	ns	ns	ns	ns	0/0	ns	0/0	0/0	0/0	1/1	0/0	0/0	0/0	0/0
SE4 ^c	Not	Not	ns	0/0	ns	0/0	1/1	0/0	1/2	1/2	0/0	0/0	1/1							
AL1 ^d	Not	Not	Not	Not	Not	ns	ns	ns	ns	0/0	1/1	1/2	1/1	1/1	1/2	1/1	1/1	1/2	1/1	1/2

Not no otters in the stretch this year, ns not surveyed

^a Otters returned to this stretch in 1989

^b Otters returned to this stretch in 1995

^c Otters returned to this stretch in 1992

^d Otters returned to this stretch in 1995

^e Number of large cub litters

^f Total number of large cubs present in the stretch

year. We can conclude that some stretches were more important than others as otter breeding and cub rearing sites.

Between-stretch factors affecting otter abundance and breeding success

All the concerned variables and correlations were not affected by autocorrelation and could be considered as independent. The univariate analyses showed that AdDOtter/km correlated with some chemical and physical water variables (Log(TMIN): $r=0.708$, $P=0.016$; (TMAX)^{1/2}: $r=0.561$, $P=0.050$; Log(COND): $r=0.877$, $P=0.001$; NO₂⁻: $r=0.671$, $P=0.024$; Log(SULPH): $r=0.797$, $P=0.005$; (WATEM)^{1/2}: $r=0.850$, $P=0.002$), water dynamics and habitat structure (FLTYP: $r=0.702$, $P=0.017$; PONDS: $r=0.785$, $P=0.006$; ISLAR: $r=0.650$, $P=0.029$; HELOP: $r=0.613$, $P=0.040$; STRUC: $r=0.804$, $P=0.004$; JUNCT: $r=0.590$, $P=0.047$), system stability ($r=0.689$, $P=0.020$), presence of reservoir tails (RTAIL: $r=0.627$, $P=0.035$), ecosystem production (Log(CHLOROPH): $r=0.865$, $P=0.001$) and food abundance ((SP>5%)^{1/2}: $r=0.933$, $P<0.0001$; FISH: $r=0.892$, $P=0.001$; (FOOD)^{1/2}: $r=0.774$, $P=0.007$).

Mean number of large cub per kilometre per year also correlated significantly with ALTITUDE ($r=-0.639$; $P=$

0.032), some chemical and physical water variables (Log(COND): $r=0.862$, $P=0.001$; Log(NO₃⁻): $r=0.762$, $P=0.034$; NO₂⁻: $r=0.762$, $P=0.009$; Log(SULPH): $r=0.831$, $P=0.003$; (WATEM)^{1/2}: $r=0.692$, $P=0.019$), water dynamics and habitat structure (FLTYP: $r=0.776$, $P=0.007$; PONDS: $r=0.793$, $P=0.005$; ROCKY: $r=0.596$, $P=0.045$), frequency of perturbations (BIGUP: $r=-0.731$; $P=0.013$), ecosystem production (Log(CHLOROPH): $r=0.864$; $P=0.001$) and food abundance ((SP>5%)^{1/2}: $r=0.742$, $P=0.011$; FISH: $r=0.865$, $P=0.011$; Log(CRFISH): $r=0.777$, $P=0.007$; (FOOD)^{1/2}: $r=0.961$, $P<0.0001$).

It is noteworthy that (FOOD)^{1/2}, FISH and Log(CRA-FISH) were significantly correlated with Log(CHLOROPH), demonstrating that the amount of food was also determined by ecosystem production. Moreover, Log(CHLOROPH) was significantly correlated ($P<0.05$) with some water-related parameters such as (WATEM)^{1/2}, Log(COND), Log(SULPH), NO₂⁻ and Log(NO₃⁻), air temperature (Log(TMIN), (TMAX)^{1/2}) and ALTITUDE.

Most physical and chemical water variables were correlated with ALTITUDE ($P<0.049$), such as Log(TMIN), (TMAX)^{1/2}, Log(COND), (%O₂), Log(SULPH) and (WATEM)^{1/2}. Other interesting correlations appeared for NO₂⁻ (with PHOSP and Log(NO₃⁻), STRUC (with DEPTH, POND, ISLAR and FLOW), WATER (with

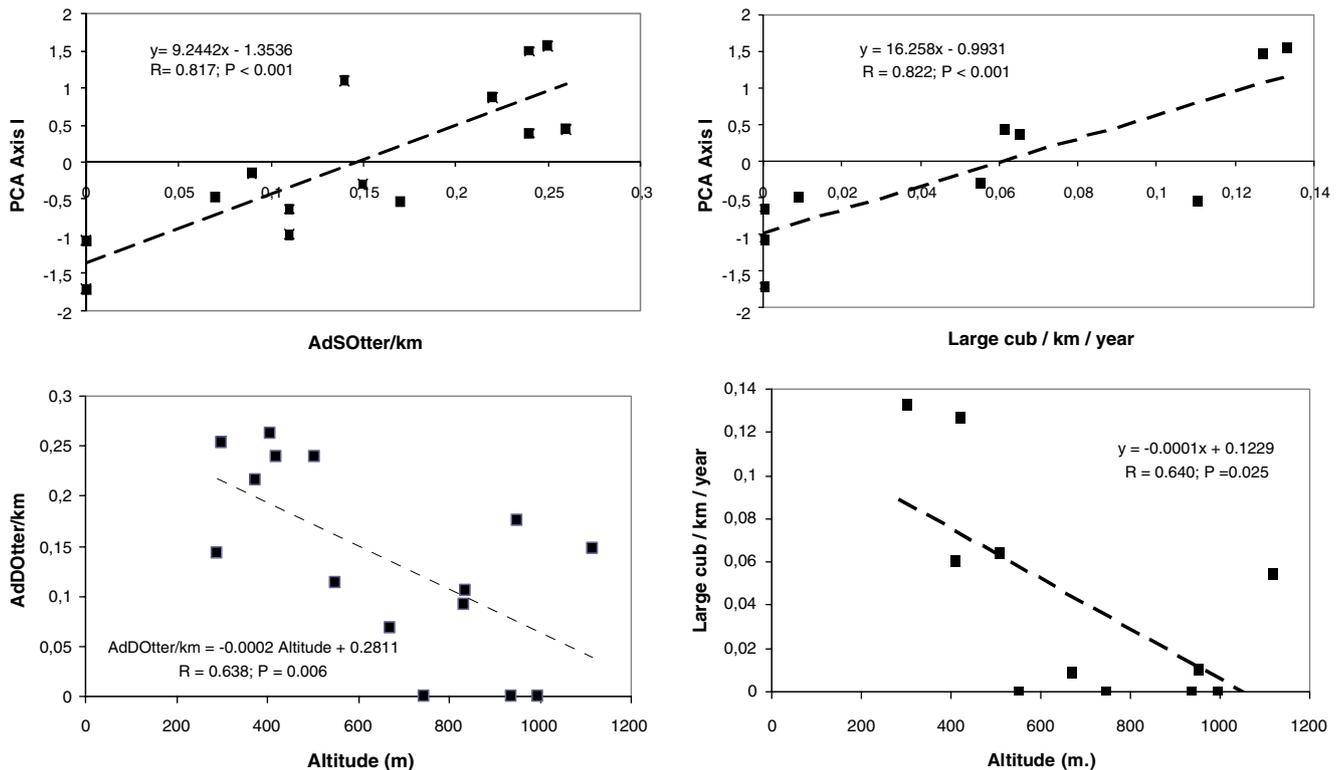


Fig. 4 Relationship between mean otter abundance index, AdDOtter/km (*left*) and otter breeding index, large cub per year per kilometre (*right*) and the PCA axis I (*top*) and ALTITUDE (*bottom*) for the stretches studied

FLTYP) and $FOOD^{1/2}$ (with $SP > 5\%$, FISH, $\text{Log}(\text{CRFISH})$, PONDS, ROCKY, BIGUP and HELOP).

The first five components of the PCA accounted for 88% of the variance (41.3%, 18.5%, 13.7%, 9.3% and 6.1%, respectively). Axis I correlated significantly with AdSOtter/km and large cubs per year per km (Fig. 4). It was very demonstrative, as this axis gave way to the grouping of data according to an altitudinal gradient (Fig. 4). In agreement with this finding, the attribute ALTITUDE significantly correlated with otter abundance and large cub per kilometre per year, highlighting the gradient that also follows both otter parameters (Fig. 4). Axis II grouped the data according to the water characteristics (such as its dynamics and physical and chemical properties).

PCA and univariant analyses allowed us to reduce the number of attributes for a more detailed analysis. Thus, the AdDOtter/km, large cubs per kilometre per year,

ALTITUDE, WATER, NO_2^- , $\text{Log}(\text{CHLOROPH})$, STRUC and $FOOD^{1/2}$ variables were considered in further analyses.

When using the stepwise linear regression method for AdDOtter/km, single factor dependence appeared ($F = 29.67$, 1 *df*, $P < 0.0001$; Fig. 5):

$$\text{AdDOtter/km} = 0.340\text{Log}(\text{CHLOROPH}) + 0.002$$

$$(r = 0.834, P < 0.0001).$$

There was also a single factor dependency for the mean number of large cubs on $(\text{FOOD})^{1/2}$, which was therefore also included in the model ($F = 88.18$, 1 *df*, $P < 0.0001$; Fig. 5):

$$\text{Largecubs/km/year} = 0.076(\text{FOOD})^{1/2} - 0.093$$

$$(r = 0.958, P < 0.0001).$$

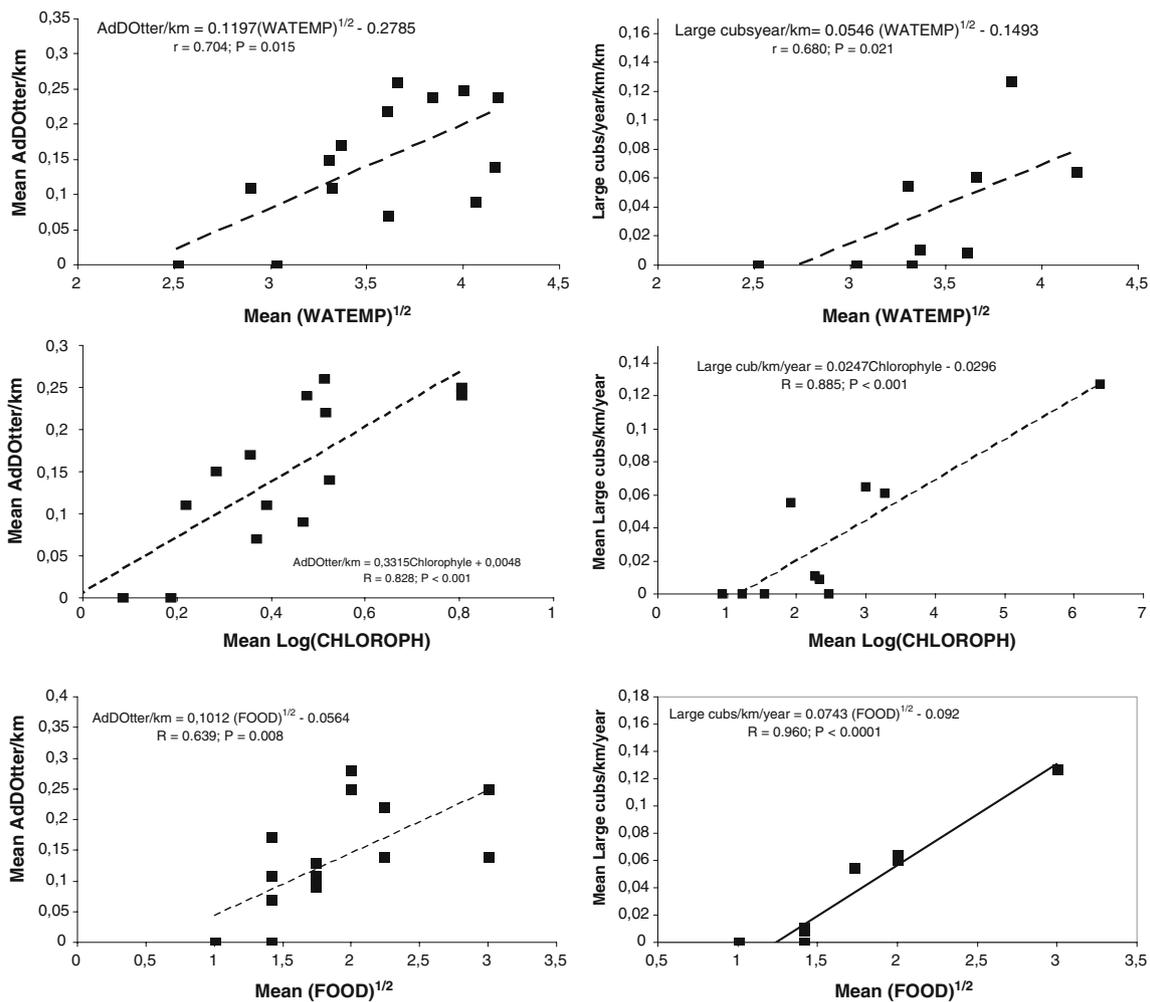


Fig. 5 Relationship for the 15 studied stretches, between the mean adult and subadult (non-cub) otter abundances (AdDOtter/km; *left*) and the mean otter breeding success (large cubs per kilometre per

year; *right*) and the main attributes explaining both parameters: mean water temperature (WTEMP; *top*), river productivity (chlorophyll a, CHLOROPH; *middle*) and food abundance (FOOD; *bottom*)

Within section factors affecting otter abundance and breeding success: the effect of perturbations

Effects of perturbations on otter abundance and breeding success were assessed for section NR1, where fish abundance was monitored for 11 years (1991, 1993–2001, 2003) and data on river flow dynamics were available for 16 years (1991–1997, 2001–2009). No autocorrelation for any variable or regression was found also for this section. No significant effect of flow—total amount of water flowing through the stretch—on AddOtter/km was found, either in the spring ($r=0.373$; $P>0.05$), the autumn previous to the visual census ($r=-0.207$; $P>0.05$), or in the entire year before the data census ($r=-0.349$; $P>0.05$). The same lack of effect was found for total flow on the number of large cubs located in the stretch ($r=0.083$, -0.443 and -0.283 ; $P>0.05$).

However, a significant correlation was found between AddOtter/km and fish biomass ($r=0.603$; $P=0.05$) and Barbel biomass ($r=0.694$; $P=0.017$), as well as between the large cubs observed per kilometre per year and fish biomass ($r=0.623$; $P=0.04$) and Barbel biomass ($r=0.693$; $P=0.04$). This was expected because Barbel accounted for 67 to 98% of fish biomass ($r=0.883$; $P<0.005$), except during some years of shortage. No significant relationship with Nase biomass appeared in any case ($P>0.05$).

Fish biomass was negatively correlated with the total flow ($r=-0.748$; $P=0.05$) in the preceding autumn, revealing an effect of floods on fish abundance. This effect does not appear with spring total flow ($r=0.358$; $P>0.05$), even considering the total flow of the year preceding the census date ($r=0.425$; $P=0.05$).

Discussion

Comments on the methods used

Field estimates on otter abundance and reproductive parameters are difficult to obtain. As for the type of methodology used here, the direct count method was previously used successfully for otter populations living in marine habitats in northern Europe (Kruuk 2006; Yoxon 2000). Moreover, visual otter censuses may be used in areas where otters are diurnal or crepuscular. This methodology has been tested by means of comparisons with data obtained from radio-tracked otters and track censuses (Ruiz-Olmo et al. 2001a, b). The direct count method is also convenient for the detection of large cubs.

The first evidence supporting the method used here is that the densities obtained lie within the habitual ranges found in the literature (Chanin 2003; Kruuk 2006). This method can also be standardised and carried out all year long, providing a very good guideline for temporal and

spatial comparisons. Nonetheless, there are some limitations. The method is much more accurate when areas with high or medium otter densities are monitored because (a) there is a higher probability of observing a proportional part of the population within stretch borders, even considering the fact that otters move long daily distances (Jiménez 2005) and (b) it becomes easier to discern between different similarly sized animals. On the other hand, the risk of false null results increases in very low-density areas, where there is a certain probability that the few individuals living there are located just outside the stretch. But even in this case, false nulls are consistent estimations of very low densities.

Data on otter abundance in the Iberian NE

Results obtained from most of the stretches studied (0.07–0.25 AddOtter/km, ranging up to 0.55; 1.45–6.26 AddOtter/km² of otter habitat, up to 9.46) were consistent with the ranges of abundances quoted in the literature (Chanin 2003; Kruuk 2006). However, exceptions were our stretches at higher altitudes with lower values, and the higher densities (2–50 otter per square kilometre) found for some British water masses.

Otter abundance and breeding success showed gradients related to altitude, as was previously suggested in a study regarding the relation of otter food diversity and breeding frequency (Ruiz-Olmo and Jiménez 2008). Otters were more abundant (0.25 AddOtter/km) and had more cubs in the lower parts (below 500 m) of the rivers studied. At the heads of the rivers, mean otter densities were often below 0.1 AddOtter/km.

Otter densities fluctuated over the years, mainly in some Pyrenean stretches located downstream of large reservoirs. Here, a pattern of peaks every 4 to 8 years was observed. MAD was higher in such rivers, with periods of high otter densities alternating with periods of lower densities. Such fluctuations have also been reported in other areas of the Eurasian otter range, such as marine habitats in the Shetland Islands (Kruuk et al. 1993). In the other stretches of our survey, fluctuations were much lower.

We found similar otter abundance fluctuations between stretches (even if located in different rivers) when habitat characteristics and conditions were similar. Dissimilar fluctuation patterns were found (even in the nearest stretches within the same river) when habitat and environmental conditions differed. This was due to the fact that prey-species abundance was likewise similar if weather traits—temperature, rain, snow—and water dynamics and perturbations regarding flow, floods and opening of dams were similar.

Data on breeding success in the Iberian NE

When excluding narrow upstream stretches (with no breeding; Ruiz-Olmo and Jiménez 2008), 18–40% of the otters observed

during the censuses were cubs. Mean litter sizes (1.60 small cubs per litter; 1.39 large cubs per litter) were smaller than those reported in the literature (1.6–2.8) for litters observed outside of dens (Chanin 2003; Kruuk 2006). Litters do lose more or less one of every four cubs when comparing both cub classes, which is quite similar to the 18% cub mortality during the first year of life reported for the Shetland Islands (Kruuk 2006). However, differences were non-significant, showing, as a whole, a low rate of mortality at this age. Nonetheless, differences were found between stretches: In some of them, no mortality was reported, while in others half of the cubs were lost. Differences in habitat quality were reported as an explanation for this trend (Ruiz-Olmo et al. 2005).

We have also studied the recruitment of large cubs. In some stretches, otters bred almost every year, while in others breeding was occasional. We observed between 0.009 and 0.127 large cubs per stretch per year (0.1 to 1.3 large cubs per kilometre and per year). Stretches showed a very different contribution in terms of reproduction and the rearing of cubs, with differences as high as 18:1, as was previously suggested by Kruuk (2006) and Ruiz-Olmo et al. (2005). Because otters are more vulnerable in areas with low breeding rates, the species requires high-quality patches to maintain sustainability.

Factors explaining otter abundance and breeding success: the role of ecosystem productivity

Correlation between otter abundance and breeding success, when compared with altitude, was actually a consequence of the interaction of a wide range of factors also correlated with altitude. According to our results, the main variable driving otter abundance and breeding success was ecosystem production (here estimated in terms of primary production through *chlorophyll a* concentration). However, all the other factors involved related to food (number of main prey-species, total food and fish and crayfish abundance) also explain variations in otter abundance and breeding success (and also correlate with *chlorophyll a*). Therefore, these findings bring about a consistent scenario across the food chain. The effect of food species abundance (and often of one or few of the main species, such as in our case the Ebro's Barbel) on otter abundance and breeding success agrees with the findings of Kruuk et al. (1993), Ruiz-Olmo et al. (2001a, b, 2002) and Elmeros and Madsen (1999). Other water-related variables such as temperature, conductivity and concentrations of compounds linked to nitrogen and sulphur ecosystem metabolism—within the safety levels in the studied rivers—also contributed to explaining *chlorophyll a* levels, food availability, otter abundance and breeding success (thermal effect on the ecosystem production and food chains).

Some habitat features such as flow type, abundance of ponds, helophytic vegetation, river junctions, river branches and reservoir tails also contributed to explaining changes in otter population parameters. These are also habitat structures in which otters find much more predictable and abundant food, especially fish and crayfish (Ruiz-Olmo et al. 2001a, b, 2005; Ruiz-Olmo and Jiménez 2008). Also, shelter availability is especially important for females rearing cubs. Rocky systems and island abundance correlated with otter abundance and breeding success. Ponds, rocky and cave systems, islands and river branches are usually high-quality habitats selected by fish, especially *B. graellsii* (Mathews 1998; Doadrio 2001; our unpublished data).

Effect of perturbations (floods)

We found important fluctuations in otter numbers and breeding success especially in the Pyrenean stretches located below large reservoirs. As the values of most of the other variables generally remained more or less constant within those sections over the years, we focused on the fluctuations in fish abundance and the effect of floods and reservoirs in one of these stretches (NR1). No correlation was found between any of the flow or flood related parameters and the otter variables probably because the sample size was too small. However, a consistent relationship appeared from the correlation between flow in the preceding autumn (floods) and fish abundance. Autumn floods result both from rainfall and dam activity bringing about sudden changes in water levels. Flow can increase from less than 1–3 to more than 50 m³/s. In our study area, rainy autumns resulted in fewer fish stocks during the spring. This relationship was previously suggested by Ruiz-Olmo et al. (2001a, b). Perturbations from heavy floods played an important role in river ecosystems, decreasing stability and diminishing prey-species (mainly fish) abundance. As otter demographic parameters are closely related to prey-species availability, the effect of natural floods and dam activities on these species explained temporal variations in otter populations.

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