Long-term patterns in Iberian hare population dynamics in a protected area (Doñana National Park) in the SW Iberian Peninsula: effects of wheather conditions and plant cover.

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Abstract

The Iberian hare (*Lepus granatensis* Rosenhauert, 1856) is a widely distributed endemic species in the Iberian Peninsula. In order to improve our knowledge of its population dynamics, the relative abundance and population trends of the Iberian hare were studied in the autumns of 1995–2012 in a protected area (Doñana National Park) by spotlighting in two different habitats: marshland and ecotones.

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The average relative abundance was 0.38 hare/km (sd = 0.63) in the marshland and 3.6 hares/km (sd = 4.09) in ecotones. The Iberian hare population exhibited local interannual fluctuations and a negative population trend during the study period (1995–2012). The results suggest that its populations are in decline.

The flooding of parts of the marshland in June, July and October favour hare abundance in the ecotone. Hare abundance in the marshland increases as the flooded surface area increases in October. These effects are more pronounced if the rains are early (October) and partially flood the marsh. By contrast, when marsh grasses and graminoids are very high and thick (as measured using the aerial herbaceous biomass (Biomass marshland) as a proxy), the abundance of hares decreases dramatically as does the area of the marsh that is flooded (in November).

Key words: *Lepus granatensis*, trends, population dynamics, Iberian Peninsula, Doñana.

Introduction

The Iberian hare (*Lepus granatensis* Rosenhauert, 1856) is endemic to the Iberian Peninsula and is an important prey for a large number of endangered predators such as the Spanish imperial eagle (*Aquila adalberti*), Iberian lynx (*Lynx pardina*) and wolf (*Canis lupus signatus*) (Purroy 2011). In addition, it is also one of the most important game species in Spain and around one million hares were harvested during the 2010–2011 hunting season (Garrido 2011).

Iberian hares are widely distributed (Palacios 1978, Palacios & Meijide 1979) and are common in both agricultural land and non-agricultural areas, from the sea level to over 3,000 m. a.s.l. (Carro & Soriguer 2002). In the Doñana National Park, the marshland is a typical habitat of Iberian hares (Valverde 1960, 1967). In this habitat, hares are restricted during periods of flooding to the *vetas*, the scattered, slightly higher elevations (0.40–1.2 m) that range in surface area from just a few dozen square meters to a few hectares (Carro *et al.* 2011).

Trends in Iberian hare populations are unclear. In the 1990s it has declined in the north of the Iberian Peninsula (Duarte 2000), but increased in southern Spain (Duarte & Vargas 1998). Population declines have been observed in other European hare species since the mid-1960s (Hutchings & Harris 1996; Ninov 1990; Marboutin & Peroux 1995; Schmidt *et al.* 2004) and some of the factors proposed to explain these negative tendencies include the loss of habitat diversity (Dingerkus & Montgomery 2002; Tapper & Barnes 1986), hunting and predator pressure (Spittler 1987; Reynolds & Tapper 1995), agricultural intensification (Smith *et al.* 2004), disease (Edwards *et al.* 2000) and weather (Jennings *et al.* 2006; Kiliyas & Ackermann 2001; Rödel & Dekker 2012; Spittler 1987).

However, few studies have ever addressed issues regarding the ecology and population dynamics of Iberian hare populations, or the trends in and causes of its population decline. Although authors such as Andre *et al.* (1997), Batista & Cruz de Carvalho (1996), Carro *et al.* (1999), De la Calzada & Martinez (1994), Gil *et al.* (2013), Gortazar *et al.* (2007), Lazo *et al.* (1992), Lopez *et al.* (1996) and Sánchez-García *et al.* (2012) have offered partial

explanations to these questions, better understanding of the factors affecting Iberian hare abundance are still needed to improve management strategies aimed at favouring this species.

The monitoring of trends in animal populations is a key aspect of species conservation and wildlife management (Buckland *et al.* 1993), while long-term ecological research (LTER) is necessary for tackling the influence of ecological changes.

This paper aimed to study the effects of environment (rainfall and flooded surface area) and herbaceous vegetation biomass on Iberian hare abundance on early autumn in two typical habitats of Doñana National Park, SW of the Iberian Peninsula during the period 1995–2012.

MATERIAL AND METHODS

Study area

The study area consisted of two typical habitats occupied by the Iberian hare in the Doñana National Park (DNP) (36°56'51"N 6°21'31"O) (SW Iberian Peninsula) (Fig. 1): the **Ecotone** (La Vera), a transition area between the scrubland and the saltmarsh characterised by the plant association *Galiopalustris-Juncetum maritime* that forms a strip of variable width running across the DNP from NW to SE. It is characterized by a great diversity and abundance of plant and herbivore species (ungulates, lagomorphs). By contrast, the vegetation communities in the **Marshland** are dominated by the plant associations *Scirpetum maritimi* and *Gallium palustris* with *Juncetum maritimum*, and the presence and extent of this habitat are basically determined by micro-topography, in which the differences of level,

which are few centimeters in height, have large hydrological and ecological significance because they condition the flooding, salinity variations, and the distribution of fauna and vegetation (Castroviejo, 1993). The lowest saltmarshes areas remain flooded for the longest periods of time (up to several months).

The Doñana natural wetlands are essentially a seasonal freshwater marsh that floods in winter and dries up in summer. The natural marshes in DNP are chiefly fed by surface flow and the direct rainfall that falls in October and April-May. DNP has a total surface area of 54 000 ha: the surface area of flooded marshes exceeds 23 000 ha in relatively wet winters, but is much less in dry winters and is close to zero during in the hot summer months (Serrano et al., 2006).

The climate is Mediterranean sub-humid with mild and unpredictable rainy winter season and hot dry summers. Generally, rainfall is concentrated from October to April-May (Serrano et al., 2006). The mean annual rainfall is 550 mm/year (1978–2013).

Depending on the amount, intensity and seasonal distribution of rainfall, the marshland changes dramatically during the year, and from one year to the next. In late spring and summer it is usually completely dry and is populated by many herbivores, including hares and red and fallow deer (Carro, 2005; Soriguer et al, 2001). During the autumn-winter season, however, the marshland is flooded in most years.

Hare abundance index

The hare abundance data from 1995–2008 were gathered from Carro *et al.* (2010) and from data generated in 2009–2012 by Carro (2005) and the Natural Processes Monitoring Team

(ESPN-EBD-CSIC). In the years 1995–2012 hare abundance estimates in the DNP were obtained from fixed transects that cross the typical habitats of the Iberian hare (ecotone and marshland). The length of the transects varied due to annual variations in water levels and to restrictions imposed by the imperial eagle conservation programme on access to this raptor's nesting areas. All surveys were carried out using a 4x4 vehicle with a handheld 100-watt spotlight, always after dusk when hares are most active (Barnes *et al.* 1983; Homolka 1986). Surveys were conducted in early autumn by teams of at least two people (Barnes & Tapper 1985; Frylestam 1981,1982). In total, transect lengths of 923 km in the marshland and 145 km in ecotones (La Vera) were surveyed. One of the observers sat on the roof of the vehicle at a height of at least three meters to increase detectability and therefore sampling precision (Wywiałowski & Stottart 1988). We recorded hares by direct detection and observations were then confirmed using binoculars. We also measured the perpendicular distance of hares from the transect line using a laser telemeter (Geovid, Leica, Solms, Germany). The maximum width of the contact strip was 200 m and depended on the height of the vegetation at the time. The majority of contacts were within 100 m of the observer. Counts were postponed with dense fog, rain or strong winds made counting impracticable. The autumn 2001 surveys were only carried out in La Vera because the rains had flooded the marshland much earlier than expected.

According to Barnes and Tapper (1985), spotlighting is the best method for assessing hare populations in extensive studies. The Iberian hare inhabits by choice open land (Carro & Soriguer 2002) and, if carried out repeatedly over the same area, spotlighting in such habitats can provide a reasonably accurate measure of population changes over time. The particular

advantages of this technique include the very large area that can be covered in a relatively short period of time and the little disturbance it causes to hares. Disadvantages include biases arising from having to restrict sampling to areas close to tracks (Langbein *et al.* 1999) and the visual interference caused by the vegetation.

Barnes and Tapper (1985) give estimates that vary considerably between nights and conclude that these differences could be explained in part by a negative relationship with temperature. They detected significantly fewer hares when counts were carried out at temperatures below 15 °C, probably because fewer hares are active in the open on cooler nights. Our data were standardized – transects were only carried out at temperatures over 15 °C – and so this problem did not affect our sampling. According to Langbein *et al.* (1999), temperatures have only a minor effect on the variance between repeat counts under the same weather conditions. The detectability of hares may vary between habitats due to differences in observers and in the characteristics of the habitats. In the DNP, the ecotone and marshland are both open habitats with similar levels of visibility. During the 18 years of surveys, the same observer participated in all surveys and all the observers were highly experienced. All these improvements were taken into account in our field sampling design.

Data analysis

The hare densities were estimated using a Distance sampling (Buckland *et al.* (1993); nevertheless, due to the low number of observations during some annual surveys, we present here the results as a Kilometer Abundance Index (KAI) to facilitate comparisons between all the study periods.

Data are expressed as an index of relative abundance (KAI) that corresponds to the number of hares observed per kilometre. This index reflects the relative abundance at a given locality at a given time relative to the average for the whole monitoring area (Conroy 1996; Crawford 1991; Engeman 2005).

Food availability

The herbaceous biomass was estimated in seven herbivore exclusion enclosures in the DNP (Fig. 1). The exclusion fences enclosed an area of 20 x 20 m. In late spring and late autumn, three samples were taken from inside each exclusion zone and five samples from outside this zone at 0, 50, 100, 150 and 200 m from the enclosure. A patch of herbaceous vegetation (10 x 100 cm) was cut at ground level with electric shears and yielded a cut sample of 0.1 m². Samples were placed in a drying oven with forced ventilation at 60°C until a constant weight was obtained. The biomass is thus expressed as the weight (kg) of dry herbaceous mass per hectare (Soriguer et al 2001).

Hare abundance index trends

The TRIM software (Trends and Indices for Monitoring Data) (Pannekoek & van Strien, 2005) was used to test for long-term trends in the Doñana hare population. These models are based on the assumption of independent Poisson distributions for counts. We used the linear trends model and took into account serial correlation and overdispersion. T-tests were used to compare differences in relative hare abundances between areas and years. Differences at $p \leq 0.05$ were regarded as significant.

Nevertheless, the counts were often not independently distributed because in a particular year they also depend on the counts from the previous year (serial correlation). The generalized estimating equations approach to estimating log-linear models is reduced to the usual maximum-likelihood approach if (a) the covariance matrix of the observations equals the covariance matrix of the independent Poisson observations, (b) the overdispersion factor is 1 and (c) the serial correlation is 0. Long-term trends were determined from multiplicative trend.

The TRIM software classified the trends according to one of six categories depending on whether the rate of change over the study period was more or less than 5% per year: a strong increase or decrease (>5% per year), a moderate increase or decrease (per year), a stable trend, or an uncertain trend with large coefficients of interval. (Pannekoek & van Strien, 2005).

Meteorological and flooding data

Meteorological and flooding data were taken from the database of the Doñana Biological Station: (see ESPN-EBD-CSIC and LAST-EBD; GIS and Remote Sensing Laboratory).

Flood levels were calculated by accessing all available cloud-free Landsat MSS, TM and ETM+ images for the Doñana area during the period 1995–2012 (>300 images were consulted and processed). Images were radiometrically corrected, transformed into reflectance values and normalised to a reference image to produce the final flood masks with pixels of 30 x 30 m (details in Bustamante *et al.* 2009; Díaz-Delgado *et al.* 2006). All images were processed and the data computed in the LAST.

Statistical analysis

We applied General Linear Models (GLM) with normal distributed errors to assess the effect of the monthly floods, monthly rainfall, monthly surface flooding area and plant biomass/cover availability on the response of monthly hares abundance in the marshland and ecotones. Variables were log transformed ($\log+1$) to obtain normal error distributions.

First, we fitted a model including the all main effects and then another set of effects to derive the most significant interactions. Akaike's criterion was used to select the ten best significant models. Given that the differences between AIC models were very small and that the goal of the model fitting process was not to get the best-fitted model but, rather, the most parsimonious, simplest and biologically significant models, we tested the significance between the first 10 fitted models with an Anova (F-test). A backward/forwards step procedure and a drop-off variables procedure, based on the AIC criterion, were applied to identify non-significant explanatory variables, interactions and the main effects in the final selected models.

. The variance inflation factor (VIF) was used as an indicator of multicollinearity, and a recommended maximum VIF value of 5–10 was accepted (Hair *et al.* 1998; Rogerson 2001). GAM models and non-linear models were also tested but were rejected due to the good fit observed with linear models. The statistical analyses were carried out with R 3.0.2 Statistical Software (R Core Team 2013).

Results

The total sampling effort covered 1068 km and 919 hares were counted in total (596 hares in ecotone and 323 hares in marshland). The highest indices of hare abundance were recorded in 2001 (in the ecotone) and in 1995 (in the marshland). With the exception of the years 1996, 2003 and 2005, abundances of over one hare/km were always recorded in the ecotone (Fig. 2).

In the ecotone, the average hares abundance was 3.6 (SD: 4.09), while in the marshland it was 0.38 (SD: 0.63). Yearly Iberian hare abundances were not correlated between marshland and ecotone (Spearman's r correlation: $r_s = 0.28$; $n = 18$, $p = 0.26$).

The highest hares abundance in the marshland during the study period was observed in 1995.

Population trends and models

To test its fit, we started with a model with change-points at each time-point. The goodness-of-fit for this model gave 16.10 ($df = 17$; $p = 0.51$; model not rejected). The Wald-test for the significance of deviations from linear trends was significant (Wald-test: 39.81, $df = 16$, $p < 0.001$). The estimated serial correlation was very low (0.05), while the estimated overdispersion was close to one (0.95).

The indices from 1996 to 2012 were markedly lower than those for the previous year (1995). In 2007, the population of hares increased in comparison to all other years except 1995. These differences were mainly due to an abundance peak in the autumn of 1995: in that year, indices as high as 2 hares/km were recorded in the marshland. In 1996 the population crashed following a year of heavy rain that ended the drought that had lasted from 1992 to 1996. The

highest Iberian hare abundances were found in the ecotone in 2001 (14.1 hares/km) (Fig. 2) when the marshland was flooded.

The hare population increased sharply in 1999 (201%), 2001 (301%) and 2002 (168%); nevertheless, since 2003 the species' populations have decreased by 88% in the DNP, according multiplicative parameters (Table 1).

Globally, the hare population in the DNP underwent a moderate decline in the period 1995–2012 (cf. multiplicative model: 0.93; SD: 0.034, $p < 0.05$).

In the ecotone, the most significant model had an AIC= 4.045 and a $R^2 = 0.6480$. The flooding of the marsh in June, July and October favoured the abundance of hares in the ecotone (see Table 2). This effect increases when flooding continues throughout July (interaction LogMSI_{June}: LogMSI_{Jul}). In the marshland, the most significant model (Table 2) had an AIC= 10.101 and a $R^2 = 0.7094$. Hare abundance in the marshland increases as the flooded surface area increases in October.

These effects are more pronounced if the rains are early (October) and partially flood the marsh. By contrast, when marsh grasses and graminoids are very high and thick (as measured using the aerial herbaceous biomass (Biomass marshland) as a proxy, Figure 3), the abundance of hares decreases dramatically as does the area of the marsh that is flooded (in November).

The models with Total hares abundance (Ecotones + Marshland) were not significant. No significance relationship were found between LogKAI overall and the explanatory monthly flooding variables, rainfall and plant biomass (Table 2).

Discussion

This is the first long-term study of the factors affecting population trends in the Iberian hare.

We observed significant changes and declines in Doñana hare populations, both in number and in their spatial distribution in relation to flooded areas and the recolonization difficulties of the previously occupied areas. In the DNP, Iberian hares exhibit a similar marked negative trend to that detected in Iberian hares (Duarte, 2000, Ballesteros *et al.* 1996) and brown hares in other Europeans regions (Böckeler *et al.* 1994; Mary & Trouvilliez 1995; Tapper & Parsons 1984).

Our results provide evidence of the impact of weather conditions on the population dynamics of the Iberian hare, as reported by Rödel & Dekker (2012) to European rabbits and European hares. In large-scale studies, KAI estimates are commonly used to monitor and compare trends in populations rather than to compare population densities (Williams *et al.* 2007). After a widespread and high abundance of the hares in the marshland at the middle of the 90', since 1995 the hare population in the marshland collapsed and suffered great changes from year to year. A significant decline in the Iberian hare population at the study site was observed, which could be attributable to changes in vegetation cover and floods. During the five winters before 1996, the marshland suffered from an intense drought. Flooding was very rare and affected only very small areas, and so hares were widely distributed and present in large numbers. In 1997, however, there was a dramatic drop in the abundance index due to heavy rainfall and subsequent flooding. After the long droughts of 1999–2000, a widespread

peak in Iberian hare abundance occurred in 2001 in the ecotone after a series of rainy months obliged hares to move from the marshland into the ecotone (Carro *et al.*, 2011).

Stable Iberian hare populations mainly occur in the ecotone pastureland between the marshland and the scrubland that is characterized by high levels of productivity and green pastures almost all year round (Soriguer *et al.* 2001) and where the effects of flooding are less severe or none. After long periods of overgrazing the marshland becomes to be less productive (Soriguer *et al.* 2001), the vegetation cover decreases by continuous overgrazing and decay and hares slowly recolonize from the ecotone and other higher areas. During the winter, in years of heavy rainfall and sudden flood, vast areas of the low-lying marshes (>80%) and parts of the higher marshes – and even the ecotone pastures – flood. In this case, the hares that inhabit the marshland and ecotone area (physically connected to the scrubland) take refuge in the higher drier areas in the nearby scrubland. Alternatively, some of the hares living in the middle of the marshland are confined to the small elevated ‘islands’ within the marshland itself (Castroviejo 1993, Carro *et al.* 1999).

The DNP population of Iberian hares has declined markedly during the last decade. The weather (flooding) and physical barriers such as plant biomass (considered as a proxy of plant cover and plant height) have been identified as proximal factors that influence or limit hares’ recolonization and distribution in the marshland. The seasonal and inter-annual displacement of hares to higher sites (marshland islands and ecotone zones) during flood periods not only reduces hares’ distribution but also increases their availability to predators since they are restricted to very small refuges with no aerial protection. According to Carro (2005), the Iberian hare has low survival rates in the marshland (38%) where all mortality is observed in

flood season. In the ecotone survival rates are lower (22%) and mortality is observed throughout the year. Hares are often preyed upon by raptors and mammals in the DNP (Carro 2005). As observed in Iberian Hare, factors such as poor body condition during periods of isolation in poor quality refuges and disease (Alzaga *et al.* 2007) also help explain this negative trend. Ours data during the winter capture and mark confirm these previous results.

The main factors in the marked declines in European brown hare populations are considered to be human activities, predators, disease and climate (Edwards *et al.* 2000; Schmidt *et al.* 2004). In DNP, the abundance of Iberian hares in the marshland increases with the increase in flooded area in October. These effects are more pronounced if rains fall early in October and partially flood the marsh. By contrast, in November, when marsh grasses and graminoids are very high and thick (as measured using the aerial herbaceous biomass as a proxy), hare abundance in the marshland decreases dramatically, as does the flooding of the marshland. High values of herbaceous plant biomass (taken as a proxy of plant cover and plant height; Röttgermann *et al.*, 2000) and flooded surface area in the marshland have a very negative impact on Iberian hare abundance in the marshland (recolonization and survival). The flooding of the marsh in June, July and October favours hare abundance in the ecotone. This effect increases when flooding continues throughout July.

KAI methods that can be used by rangers and wildlife managers are useful and affordable tools for monitoring Iberian hare populations. The Iberian hare population should continue to be studied because such long-term monitoring is required to assess the impact, for example, of global change, management practices, loss of habitat, hunting pressure and prey availability for predators.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

FC and RS contributed to the conception, design, data collection, laboratory work, data analysis, drafting and writing of the manuscript.

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Table 1. Averages and multiplicative slopes for each year of monitoring of the Iberian hare populations in the Doñana National Park (1995–2012) estimated using the TRIM programme.

Year	Average	Multiplicative Slope	SD
1995	2.53	1.00	
1996	0.46	0.18	0.20
1997	0.77	0.30	0.27
1998	3.13	1.23	0.72
1999	5.10	2.01	1.07
2000	3.30	1.30	0.75
2001	7.62	3.01	1.50
2002	4.27	1.68	0.92
2003	0.31	0.12	0.16
2004	0.43	0.17	0.19
2005	0.09	0.03	0.08
2006	0.66	0.26	0.25

2007	2.30	0.91	0.57
2008	2.39	0.94	0.59
2009	0.76	0.30	0.27
2010	0.55	0.22	0.22
2011	0.92	0.36	0.30
2012	0.44	0.17	0.20

Table 2. Results of the best-fit linear model predicting hare abundance in marshland in the Doñana National Park. Estimated coefficients, Standard errors, T-values, probability values, Sig: AIC: Akaike information criterion, R^2 : coefficient of determination.

Variates Response (Logaritm transformation) : KAI Marshland: kilometric abundance index of marshland; KAI Ecotone: kilometric abundance index of ecotone; KAI Total: kilometric abundance index of total KAI.

Variates explicatives (Logaritm transformation) : BiomMarsh: herbaceous plant biomass of marshland; Rainfall: Annual rainfall; MSjun: maximum flooding surface in June; MSIjul: maximum flooding surface in July; MSioct: maximum flooding surface in October; MSjun: MSIjul: Interaction maximum flooding surface in June with maximum flooding surface in July; BiomEcot: herbaceous plant biomass of ecotone; MSIapr: maximum flooding surface in April; MSiaug: maximum flooding surface in August; MSidec: maximum flooding surface in December; MSifeb: maximum flooding surface in February; MSIjan: maximum flooding surface in January; MSImar: maximum flooding surface in March; MSImay: maximum flooding surface in May; MSinov: maximum flooding surface in November; MSIsep: maximum flooding surface in September.

Response	Explanatory	Estimate	Std. Error	t value	Pr(> t)	Sig	AIC	R^2
IKAMarshland	(Intercept)	1.7900	0.3700	4.8320	0.0000	***	10.1010	0.7050
	MSioct	0.1950	0.0640	3.0660	0.0090	**		
	BiomMarsh	-0.8450	0.1640	-5.1560	0.0000	***		
	MSInov	-0.1590	0.0590	-2.6730	0.0190	*		
	Rainfall	0.4240	0.1550	0.2730	0.0170	*		
IKAecotone	(Intercept)	-9.5710	2.4060	-3.9780	0.0020	**	4.0450	0.6480

	MSIjun	2.2200	0.5130	4.3340	0.0010	***		
	MSIjul	4.1800	1.1030	3.7900	0.0020	**		
	MSIoct	0.2600	0.0670	3.8630	0.0020	**		
	MSIjun:MSIju	-1.0110	0.2430	-4.1160	0.0010	**		
IKAtotal	(Intercept)	-1.3910	5.2060	-0.2670	0.8140	ns	13.5630	0.7210
	BiomEcot	0.1980	1.1520	0.1720	0.8790	ns		
	BiomMarsh	0.1710	1.1660	0.1470	0.8970	ns		
	MSIapr	-1.9250	4.2470	-0.4530	0.6950	ns		
	MSIaug	0.5870	0.9120	0.6440	0.5860	ns		
	MSIdece	-0.0230	0.7080	-0.0320	0.9780	ns		
	MSIfeb	-0.2320	3.1370	-0.0740	0.9480	ns		
	MSIjan	0.7700	1.3490	0.5710	0.6260	ns		
	MSIjul	-1.5600	1.5480	-1.0080	0.4200	ns		
	MSIjun	1.3840	2.4000	0.5770	0.6220	ns		
	MSImar	0.4350	4.8640	0.0890	0.9370	ns		
	MSImay	0.2390	3.2940	0.0730	0.9490	ns		
	MSInov	0.0910	0.6050	0.1510	0.8940	ns		
	MSIoct	0.1700	0.7740	0.2190	0.8470	ns		
	MSIsep	-0.1580	0.8190	-0.1920	0.8650	ns		
	Rainfall	0.5400	2.5930	0.2080	0.8540	ns		

Figure 1. Transect route in the Doñana National Park: 1. La Vera, 2. The marshland. Square: herbivorous fences enclosure.

Figure 2. Annual evolution of the KAI of Iberian hares and rainfall in the Doñana National Park (1995–2012).

Figure 3. Annual biomass production in marshland and ecotone.